

DECREASE OF AFRICAN PENGUINS AT THE POSSESSION ISLAND GROUP, 1956–1995: CONTRASTING TRENDS FOR COLONIAL AND SOLITARY BREEDERS

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SUMMARY

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Between 1956 and 1995, the African Penguin *Spheniscus demersus* population at Possession Island decreased by 96% from 23 245 breeding pairs to 895 pairs. At adjacent North Reef, African Penguins ceased breeding before December 1988. In 1956, 850 pairs bred there. At Possession Island, 22 441 pairs of penguins bred colonially in 1956, but there were only 360 pairs in colonies in 1995 – a decrease of 98%. By contrast, there were 804 solitary breeding pairs in 1956 and 535 in 1995 – a decrease of 33%. All colonies at the southern portion of Possession Island and that at North Reef were abandoned by 1986. In the central and northern portions of Possession Island colonial breeding still persists, but as numbers have decreased colonies have fragmented. Minimal recruitment to the breeding population, probably resulting from food scarcity, is considered the most likely reason for the long-term decrease in penguin numbers. When penguins were abundant, there were insufficient suitable sites for solitary breeding and most birds bred in large colonies. Sites used by solitary breeders provide shade and restrict access by predators. Colonial breeding may have facilitated sharing information on the distribution of, and group foraging on, Sardine *Sardinops sagax*, the main food of penguins off Namibia in the 1950s.

INTRODUCTION

Possession Island (27°01'S, 15°12'E) and adjacent North Reef (27°00'S, 15°11'E), which form the Possession Island group, lie 2.7 km off the southern Namibian coastline. In 1956, there were 46 000 adult African or Jackass Penguins *Spheniscus demersus* at Possession Island and 3500 at North Reef (Rand 1963). By 1967, the number at Possession Island had fallen by 60% to some 18 000 adults. However, the island was then still the most populous breeding locality for the species along the Namibian coast (Shelton *et al.* 1984). By the late 1970s, there were about 8000 adults at Possession Island, a number exceeded by both Ichaboe and Mercury Islands (Crawford *et al.* 1995b). By the late 1980s, the population at Possession Island had dropped to 3000 adults and the locality was fourth most important for the species in Namibia, behind Halifax Island. In the early 1990s, there were fewer than 3000 adult penguins at Possession Island (Crawford *et al.* 1995b).

At North Reef, there were 500 adult penguins in the late 1970s, but less than 200 in the early 1980s (Crawford *et al.* 1995b). Penguins stopped breeding at North Reef after 1987 (Crawford *et al.* 1995a).

African Penguins at Possession Island nest in colonies, on the island's surface or in self-excavated burrows in guano, and solitarily, under bushes, rocks or man-made structures and in burrows, as they did at North Reef (Rand 1963, pers. obs.). The rates of decrease in the numbers of pairs in and outside colonies have been vastly different. In this paper we document these trends, and comment on possible reasons for their

discrepancy. We also consider reasons for the large decrease in numbers of penguins.

METHODS

Aerial photographs of Possession Island and North Reef were taken on 21 November 1956 (Rand 1963), 14 November 1967, 28 November 1978, 9 July 1979 (Shelton *et al.* 1984), 20 December 1993 and 18 December 1995. Aerial photographs of a central portion of Possession Island were taken on 9 December 1980, 14 December 1981, 28 November 1982, in December 1983, on 19 December 1984, in December 1985, on 21 December 1987, 20 December 1988, in December 1989, on 20 December 1992 and 19 December 1994. Numbers of African Penguins at discrete colonies were counted on enlarged prints of the first two surveys. Details of photographic techniques used and methods of counting are given by Shelton *et al.* (1982, 1984).

The Possession Island group was visited during December 1978, December 1985, October/November 1986, September 1987, November 1987, February 1988, December 1988, January 1993 and December 1995 (Crawford *et al.* 1995b). North Reef was not visited in February 1988, but it was in March 1991 (Crawford *et al.* 1995a, 1995b). During visits, counts were made of the numbers of active nest sites at discrete colonies, except in 1986 when counts for some colonies were combined, and of the numbers of active solitary nests. At Possession Island, numbers of solitary nests were recorded separately for the southern region and for the remainder of the island, and in many of the

counts for eight separate regions (Fig. 1), allowing inter-region comparisons of trends. Methods of counting were the same on each survey, and are described by Shelton *et al.* (1984) and Crawford *et al.* (1990). During ground surveys, the locations of colonies were mapped. More accurate maps were compiled later with the aid of aerial photographs taken during the same year, when these were available.

Numbers of pairs of penguins breeding at colonies in 1956 and 1967 were estimated by dividing counts obtained from aerial photographs by 1.6, in accordance with the observation of Rand (1963) that 40% of mates were generally absent from colonies. Similarly, the number of pairs of solitary breeders in 1956 was estimated by dividing Rand's (1963) count of solitary breeding birds by 1.6. This factor was checked by comparing counts of penguins on aerial photographs taken on 28 November 1978 with ground counts of nests of colonial breeders made during 1–7 December 1978. A ratio of 1.7 was obtained for both Possession Island and North Reef. Therefore, use of Rand's (1963) ratio may have slightly overestimated (by about 6%) the number of breeding pairs in 1956 and 1967, and hence the decrease between these dates and 1978.

As a check on trends obtained from counts, the surface areas of colonies photographed from the air were measured on

enlarged prints taken in 1956, 1967, 1978 and 1995, using a compensating polar planimeter equipped with a tracing magnifier. Each area was measured three times and the mean used.

The overall rates of decrease of colonial and solitary breeders were compared. The decreases at Possession Island in the total number of breeding pairs, and in number of pairs nesting colonially, were modelled by the equation:

$$P_t = P_0 e^{-Mt} \quad (1),$$

where P_t = number of pairs breeding in year t ,
 P_0 = number of pairs breeding in 1956,
 t = years elapsed since 1956,
 e = the natural exponent (2.718 ..),
 M = the natural mortality rate.

Fitting the equation provided estimates of the natural mortality rate, and hence of the survival rate of breeders, given the assumption that there is no recruitment to, or emigration from, the breeding population. The latter assumption is likely to hold because adults generally do not breed at more than one island (Randall *et al.* 1987). However, it is unlikely that there was no recruitment to the breeding population. Recruitment to the

TABLE 1

Estimated numbers of pairs of African Penguins breeding solitarily or in colonies at various parts of Possession Island and at North Reef, 1956–1988

	21 Nov 1956 ^{1,2}	14 Nov 1967 ^{1,3}	1–4 Dec 1978	4–8 Dec 1985	30 Oct– 2 Nov 1986	4 Sep 1987	28–29 Nov 1987	25–26 Feb 1988	4–5 Dec 1988	29–31 Jan 1993	5–7 Dec 1995
Solitary breeders											
Possession											
South	239	–	126	125	37	111	31	44	94	120	176
Centre & north	565	–	239	120	28	115	67	64	150	149	359
Overall	804	–	365	252	65	226	98	108	244	269	535
North Reef	156	–	0	0	0	2	1	–	0	0	0
Colonial breeders											
Possession											
South	4571	1218	419	3	0	0	0	0	0	0	0
Centre	12229	4197	797	263	199	178	197	301	368	232	266
North	5641	2128	987	120	63	38	159	204	334	168	94
Overall	22441	7543	2203	386	262	216	356	505	702	400	360
North Reef	694	243	151	0	0	0	0	–	0	0	0
All breeders											
Possession	23245	>9081	2568	638	327	442	454	613	946	669	895
North Reef	850	>243	151	0	0	2	1	–	0	0	0

¹ Number of breeding pairs estimated as 0.625 count of penguins (Rand 1963).

² Census reported by Rand (1963), but original photographs recounted to obtain proportions of birds breeding at the south, centre and north of Possession Island.

³ Census reported by Shelton *et al.* (1984), but original photographs recounted to obtain proportions of birds breeding at the south, centre and north of Possession Island.

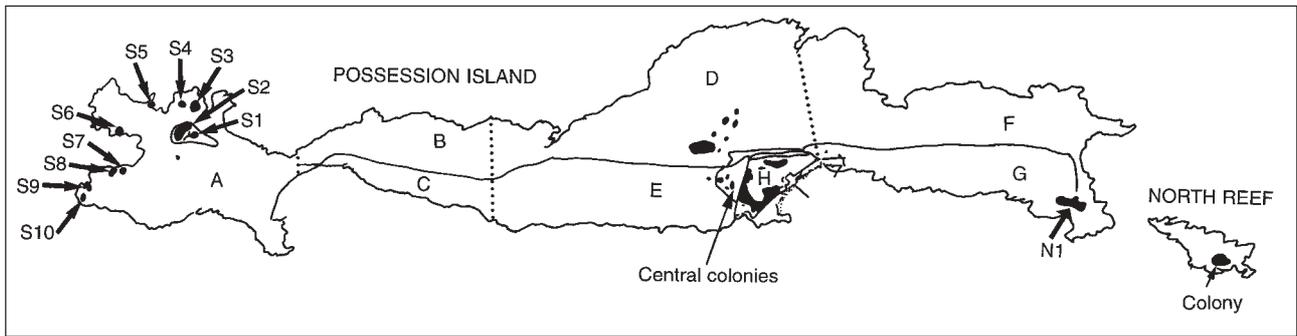


Fig. 1. Possession Island and North Reef showing the locations of colonies of African Penguins illustrated in greater detail in Figs 3–6, the locations of other small colonies at the southern end of Possession Island (S3–S10), and the subdivision of Possession Island used in the counts of solitary breeding pairs (areas A to H).

population will cause mortality to be underestimated, and survival to be overestimated.

In January 1993, the numbers of pairs of penguins that nested under bushes, under rocks, in buildings, in burrows and in the open were established, for those that bred in colonies and those that nested solitarily, to investigate differences in site selection by colonial and solitary breeders.

RESULTS

Population trend

At North Reef, there were an estimated 850 breeding pairs of African Penguins in 1956, of which 82% were in a colony. In December 1978, there were 151 breeding pairs in this colony, but none was apparent at the colony on an aerial photograph taken in July 1979, early in the breeding season (Crawford *et al.* 1995b). No colonial breeding was recorded after this date (Table 1). A few solitary pairs bred at North Reef until November 1987, after which breeding stopped (Crawford *et al.* 1995a).

At Possession Island, the estimated number of breeding pairs decreased by 96% from 23 245 in 1956 to 895 in 1995 (Table 1). The lowest counts of breeding birds (<650 pairs) were made between 1985 and 1988, since when there was a slight increase. Patterns of decrease were different for colonial and solitary pairs.

TABLE 2

Areas (m²) of colonies of African Penguins breeding on the surface at various parts of Possession Island and at North Reef, 1956-1995

Area	Nov 1956	Nov 1967	Dec 1978	Dec 1995
Possession				
South	3463	1559	280	0
Central	8341	5238	861	186
North	6049	3754	1732	118
Overall	18033	10551	2873	304
North Reef	544	320	184	0

Colonial breeders

Between 1956 and 1995, numbers of colonial breeders decreased by 98% from 22 441 to 360 pairs (Table 1). The lowest count was of 216 pairs on 4 September 1987. This is early in the breeding season (Crawford *et al.* 1995b) and not all pairs may have initiated breeding. There was a recovery to more than 700 pairs in 1988, and then a return to the low levels of the mid 1980s.

In 1956, the area occupied by penguin colonies at Possession Island was about 18 000 m² (Table 2). This fell to less than 3000 m² in 1978 and just 304 m² in 1995. Between 1956 and 1995 there was an overall decrease of 98% in the area occupied by penguins breeding in colonies on the surface, identical to the decrease in counts of pairs breeding at colonies. Some colonies have used burrows, at least since 1978 (Table 3). In 1956, the colony at North Reef occupied 544 m².

The surface area of colonies was significantly related to counts of the number of breeding pairs they supported (Fig. 2, $r = 0.941$, $n = 14$, $P < 0.001$).

During their decrease, the larger colonies frequently fragmented into a number of smaller colonies (Figs 3–5). In the course of fragmentation of colonies, it was sometimes difficult

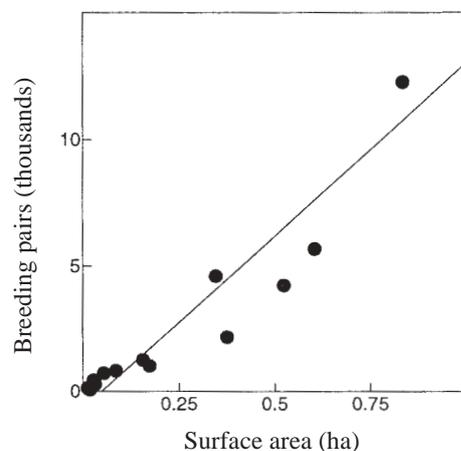


Fig. 2. The relationship between the number of breeding pairs of African Penguins in colonies at Possession Island, and the area occupied by the colonies.

Fig. 3. Changes in the extent of the colony of African Penguins at the north of Possession Island, 1956–1995.

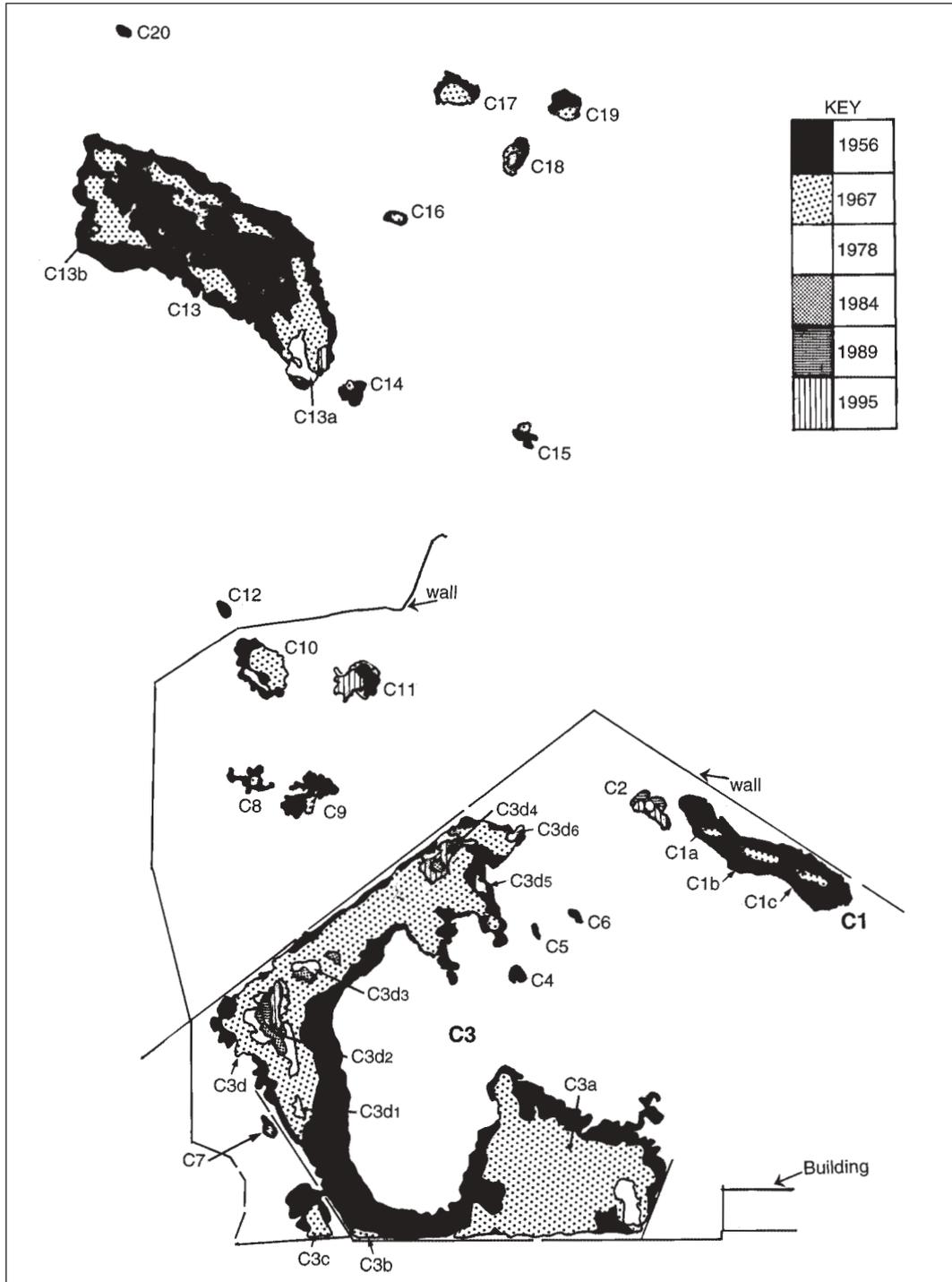
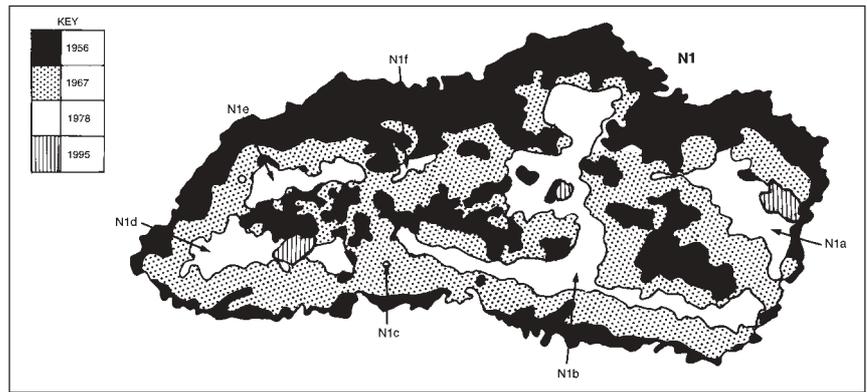


Fig. 4. Changes in the extent of colonies of African Penguins at the centre of Possession Island, 1956–1995.

at the centre of Possession Island to attribute splinter colonies to parent colonies given the lengthy gaps between visits and aerial surveys. Table 3 represents our best interpretation. Some colonies maintained their integrity as they decreased, for example that at North Reef (Fig. 6). Breeding at some colonies, e.g. N1e (Table 3), appears to have stopped and later recommenced. Breeding has also been established at a new area (C2) adjacent to the distribution of existing colonies (Fig. 4). It seems likely that this resulted from movement of birds from decreasing colonies, e.g. C3.

Solitary breeders

Between 1956 and 1995, solitary breeders at Possession Island decreased by 33% from 804 to 535 pairs (Table 1). The lowest count, just 65 active sites, was recorded in 1986, at which point the estimated decrease since 1956 was 92%. However, there was a subsequent large increase in the number of solitary breeders. In 1995, the number of solitary pairs at the south of the island (area A) was 75% of the 1956 level. Over the remainder of the island, the number of solitary breeders was 63% of its 1956 level (Table 1).

Since 1978, the number of solitary breeders has increased by 46% (Table 1). This is mainly attributable to a large increase in area D, from just 12 nests in 1985 to 201 in 1995. Most of this increase took place after 1988 (Table 4). Between 1978

and 1995 there was an increase of 51 solitary pairs in area A, mostly after 1993 (Table 4).

Rate of decrease

Between 1956 and 1987, there was an exponential decay in the overall number of penguins breeding at Possession Island, as well as in the number of pairs breeding in colonies (Fig. 7). Application of equation (1) yielded estimates of $M = 0.125$ for the overall population ($r = 0.974$, $n = 6$, $P = 0.001$) and $M = 0.136$ for colonial breeders ($r = 0.977$, $n = 6$, $P < 0.001$). These estimates are respectively equivalent to proportions of 0.88 and 0.87 surviving annually.

Site selection

In January 1993, 54% of the breeding pairs were nesting on the surface, 38% under bushes, 7% in burrows and 1% under rocks or in an old building (Table 5). All of the surface breeders and 40 of the pairs in burrows were in colonies.

DISCUSSION

Causes of population decrease

Between 1956 and 1995, there was a massive decrease in African Penguins breeding at the Possession Island group, from some 24 000 pairs to fewer than 1000. Using the mean ratio of 3.2 birds in adult plumage for each breeding pair at Robben Island (Crawford & Boonstra 1994), this loss translates to some 74 000 adult penguins. The cause for this decrease remains unknown. Various factors have been

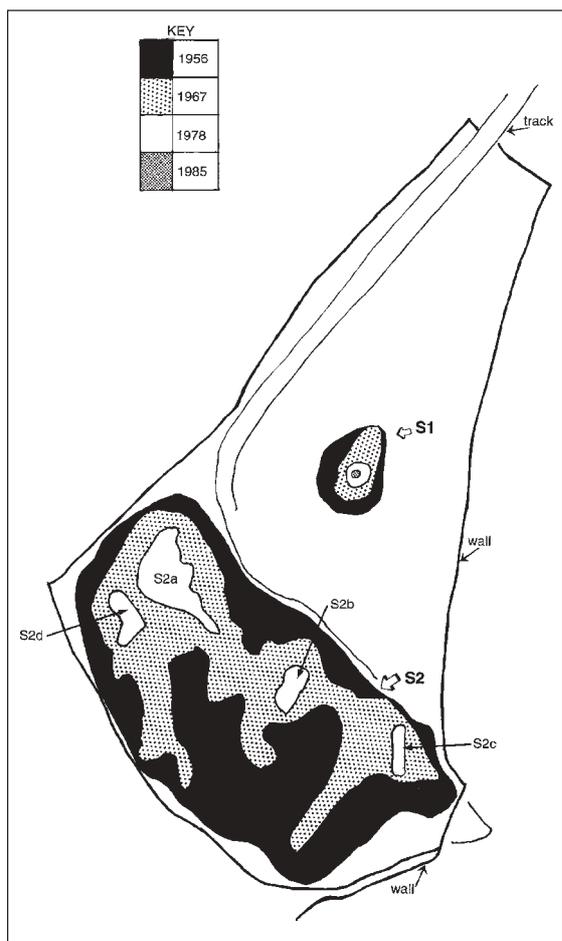


Fig. 5. Changes in the extent of the main colonies of African Penguins at the south of Possession Island, 1956–1985. The last colony in this region became extinct sometime between December 1985 and October 1986.

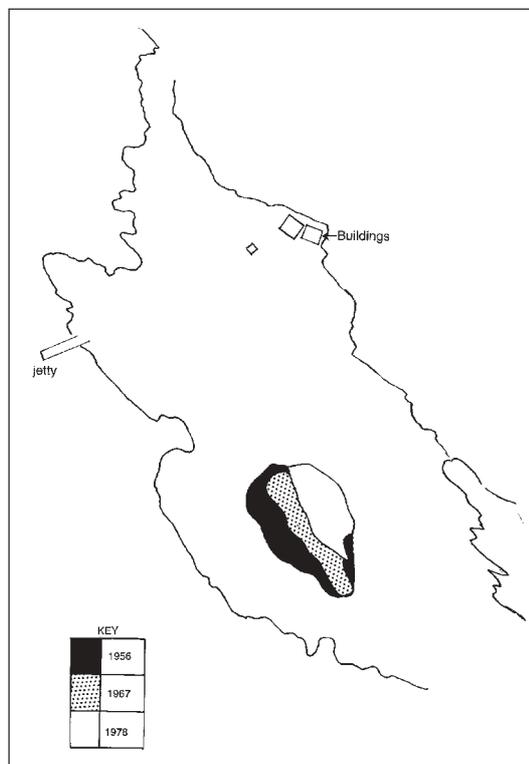


Fig. 6. Changes in the extent of the colony of African Penguins at North Reef, 1956–1978. This colony became extinct some time after 28 November 1978. No birds were at the colony on an aerial photograph taken on 9 July 1979.

TABLE 4

Estimated number of pairs of African Penguins breeding solitarily at different parts of Possession Island, 1956-1988. Subdivisions of the island are shown in Fig. 1

Area	Nov 1956	Dec 1978	Dec 1985	Sep 1987	Nov 1987	Feb 1988	Dec 1988	Jan 1993	Dec 1995
A	239	126	125	111	31	44	94	120	176
B			2	6	0	2	7	8	17
C			12	0	5	0	1	1	7
D			12	23	34		45	83	201
E			23	27	6		36	14	41
D-E			35	50	40	26	81	97	242
F			53	40			31	22	62
G			18	19			30	20	26
F-G			71	59	22	36	61	42	88
B-G	565	239	120	115	67	64	150	148	354
H		0	7	0	0	0	0	1	5

implicated in a large decrease of the overall population of African Penguins in the 20th Century, including egg harvests, guano scraping, disturbance, predation by seals and a decreased abundance of prey as a result of fishing, environmental change or competition with seals for food (Frost *et al.* 1976, Crawford & Shelton 1978, 1981, Shelton *et al.* 1984, Crawford *et al.* 1990, 1992, 1995b). Each of these factors may have operated at Possession Island.

In 1956, 4512 penguin eggs were collected at Possession and Pomona Islands (Shelton *et al.* 1984). Guano was regularly collected at Possession Island (e.g. Crawford & Shelton 1978), probably mainly from the colonies of Cape Gannets *Morus capensis*. This will have reduced opportunity for penguins to burrow into guano. Scraping of guano at Bird Island in Algoa Bay, South Africa, caused certain sections of the Cape Gannet colony there to become basin-shaped and susceptible to flooding (Randall & Ross 1979). If excessive amounts of penguin guano were collected at Possession Island, similar flooding of nests may have resulted from the sporadic rainfall that occurs along the Namibian coast. In 1985, rain caused losses of penguin eggs and mortality of chicks at Ichaboe Island (Crawford *et al.* 1986). In 1983, there were similar losses of eggs and chicks at St Croix Island following heavy rain (Randall *et al.* 1986). Disturbance to breeding penguins may have been caused by guano collection (Frost *et al.* 1976), and through the island being used as a base by sealers (Shelton *et al.* 1984) and, more recently, by prospectors for diamonds.

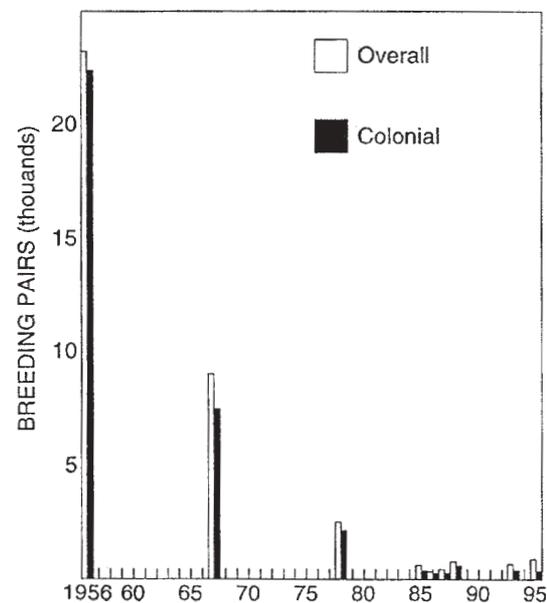


Fig. 7. Trends in the overall number of pairs of African Penguins, and in the number of pairs in colonies, at Possession Island, 1956-1995, illustrating the exponential decays between 1956 and 1987.

TABLE 5

The location of penguin nests, 29-31 January 1993

Location	Area								All areas
	A	B	C	D	E	F	G	H	
Under bush	114	8	1	77	12	21	19	0	252
Under rock	5	0	0	4	0	1	0	0	10
In building	0	0	0	0	0	0	0	1	1
In burrow	1	0	0	2	2	0	1	40	46
On surface	0	0	0	5	0	0	168	187	360

Sardine *Sardinops sagax* contributed 99% by mass of the diet of penguins off Namibia in 1957/58 (Matthews 1961). The Namibian Sardine resource collapsed in the 1960s from levels of 5–11 million tonnes between 1955 and 1965 to less than two million tonnes in 1970, and less than one million tonnes after 1975 (Thomas 1986). As the Namibian Sardine collapsed, its range contracted northwards away from Possession Island (Crawford & Shannon 1988, Lluch-Belda *et al.* 1989). This would have decreased food available to penguins breeding at Possession Island. The South African Sardine stock, which probably extended into southern Namibia, collapsed in the 1960s (Crawford *et al.* 1987).

In the Benguela ecosystem, consumption of fish by Cape Fur Seals *Arctocephalus pusillus pusillus* more than doubled between 1956 and the 1980s, as herds of seals expanded (Crawford *et al.* 1992). Especially large seal colonies exist at Wolf and Atlas Bays, about 20 km north of Possession Island. These colonies are unlikely to have existed in 1820s (Best & Shaughnessy 1979) and probably formed about the 1940s (Kruger 1949, Crawford 1991). Pup production at them increased by more than 60% from 54 000 in 1972 to 88 000 in 1983 (Wickens *et al.* 1991). Not only may seals have decreased the food available to penguins, they may also have killed penguins (Cooper 1974).

Eggs were only collected at Possession Island in 1956. Collection of guano probably only took place near the Cape Gannet colonies at the centre of the island, or around colonies of Cape Cormorants, which breed around the coast (Rand 1963, pers. obs.). Disturbance to penguins should not have been excessive, especially in the period up until 1975 when collection of guano was undertaken by the then Guano Islands Division of the South African Government (Anon. 1980). This was the period of the largest decrease in penguin numbers at Possession Island.

The most likely reason for the large decrease in numbers of African Penguins at Possession Island is a greatly reduced food supply, resulting from collapses of the Namibian and South African Sardine resources (Lluch-Belda *et al.* 1989). This is consistent with concurrent decreases in populations of African Penguins over a wide range, extending from Lüderitz to Dassen Island, South Africa (Crawford *et al.* 1990). Scarcity of food for penguins at Possession Island would have been exacerbated by the very large increase in numbers of seals at Wolf and Atlas Bays, just 20 km to the north. Off Namibia, penguins and seals are both predators of schooling pelagic fish and cephalopods (Crawford *et al.* 1985, David 1987).

Rate of population decrease

Between 1956 and 1987, there was an exponential decrease in the number of penguins at Possession Island, since when the population appears to have stabilised at a low level (Fig. 7). Given the assumption of no recruitment to the breeding population between 1956 and 1987, adult survival was estimated to be 0.87 to 0.88 during this period. Some recruitment probably did take place, so these estimates are likely to be too high. Nevertheless, they fall within the range 0.82–0.90 estimated for African Penguins at Robben Island (Crawford *et al.* 1999). This suggests there was little recruitment to the breeding population of penguins at Possession Island between 1956 and 1987. The overall decrease in numbers can probably be attributed to decay of the adult population with minimal replacement. Therefore, causes for the large decrease in numbers of penguins at Possession Island should be sought either in low

reproductive output, poor post-fledging survival or emigration of immature birds to other colonies.

Some emigration of juvenile birds may have occurred, and indeed may have been expected given the northward contraction of the main range of Sardine after the 1960s (Crawford & Shannon 1988, Lluch-Belda *et al.* 1989). As numbers of penguins at Possession Island decreased, numbers at Mercury Island to the north of Lüderitz increased. However, the increase at Mercury Island, about 2000 adults between 1956 and 1995 (Crawford *et al.* 1995b), does not approach the magnitude of the decrease at Possession Island. There was some emigration to islands off South Africa. Bird S8011, banded at Possession Island as a chick on 15 September 1988 was the parent of chicks at Dassen Island in September 1996; bird V1462, banded as a chick at Possession Island in September 1987 was at Robben Island in April 1992 (P.A. Whittington pers. comm.). In addition to emigration, it is probable that there was low reproductive success or poor post-fledging survival at Possession Island in the three decades following 1956.

Colonial versus solitary breeding

The markedly lower rate of decrease in numbers of solitary than colonial breeders between 1956 and 1995 is of interest. A possible reason is a limitation of sites suitable for solitary breeders. In January 1993, all solitary pairs were nesting under bushes or rocks, in buildings or in burrows. These habitats ameliorate extreme temperatures and reduce predation of eggs and chicks by Kelp Gulls *Larus dominicanus*. Much of Possession Island has a hard surface, making burrowing difficult (pers. obs.). There are not many suitable rock overhangs to nest under, and the number of bushes is limited (pers. obs.). Almost certainly, there were insufficient suitable sites for more than a small proportion of pairs present in 1956 to breed solitarily. As a consequence, the majority of pairs nested in large colonies.

With the severe decreases that occurred, many of the colonies fragmented into smaller colonies (e.g. Figs 3–5). There were probably local movements of birds within colonies to maintain densities. Throughout the period, there was a close relationship between the number of breeding pairs and the area occupied by surface nesters (Fig. 2).

There may have been some redistribution of breeders, with birds moving from smaller colonies to larger ones, or to solitary sites. Colonial breeding first stopped at North Reef, and then at the south of Possession Island. These were the areas that supported the least numbers of colonial pairs in each of 1956, 1967 and 1978 (Table 1), and where any advantages of colonial breeding first would have been lost. After 1988, there was an increase of some 150 solitary pairs in area D (Table 4), but decreases of about 100 pairs in colonies at the centre of the island and more than 200 pairs in colonies at the north of the island (Table 1). It is likely that the increase in solitary pairs in area D resulted from movement of birds away from colonies, especially to sites under bushes. Thus, at present solitary sites, offering shade, may be the preferred nesting habitat.

Advantages postulated for colonial breeding in seabirds include reduced predation, and acquisition of information that facilitates food finding (van Vesseem & Draulans 1986). In the former instance, birds breeding solitarily or in small colonies are thought to suffer more from nest predation than birds

breeding in large colonies. Similarly, nests at the edge of colonies are thought to have a higher probability of losses to predation than nests at the centre of colonies. The more breeding is synchronised, the less losses to predation are expected to be. The food-finding hypothesis predicts that increased colony size, or increased degree of synchronisation of breeding, improves the probability of parents finding suitable food and, consequently, the survival of chicks.

Kelp Gulls are the only predator likely to have had any major impact on penguins at Possession Island. There were 274 pairs at Possession Island in 1978 (Crawford *et al.* 1982). Prior to the 1960s it was policy of the Guano Islands Division to destroy Kelp Gull eggs and chicks and to poison or shoot adults (Crawford *et al.* 1982). This practice was discontinued at most islands in the early 1960s, but it continued in limited form at Possession Island at least until 1978 (E. Johnstone, former headman at Possession Island, pers. comm.). Although Kelp Gulls were probably never abundant at Possession Island between 1950 and 1978, their predation on eggs and chicks of penguins would have been minimised by birds nesting under bushes and rocks or in burrows, and by surface-nesting penguins gathering in large colonies.

When food is unevenly distributed and unpredictable, it is thought that birds may learn about good feeding areas by observing the flight direction and success of individuals nearby (Erwin 1978). African Penguins generally land at the same beaches (Crawford *et al.* 1989), so information on the location of food may not be obtained by observing their incoming direction of travel. Some other mechanism may occur, if information on the whereabouts of food is shared.

Sardines frequently congregate in tightly-grouped, mobile schools (e.g. Hampton *et al.* 1979). There would be advantage for penguins in knowing in which direction these schools lay, and it is conceivable that the large colonies of the 1950s facilitated the sharing of such information. In 1980, Sardine was not found in the diet of penguins at Possession Island. Cephalopods contributed 93% by number of prey items eaten (Crawford *et al.* 1985). With a change in the food base, advantages in sharing information on the location of prey schools may have lessened.

Additionally, there may have been advantage in groups foraging on schooling prey, such as Sardine, whereas had groups hunted cephalopods there may have been competition between penguins for food. More information is required on whether or not the cephalopods fed on by the penguins school, as well as on feeding strategies used by African Penguins for different prey items.

Concluding remarks

The main factor in the massive decrease of African Penguins at the Possession Island group has probably been poor recruitment of new breeders to these islands. The most likely reason for this is a greatly reduced availability of food, resulting from collapses of the southern African Sardine stocks. When penguins were abundant at Possession Island and North Reef, there were insufficient suitable sites for solitary breeding and most birds bred in large colonies. Sites used by solitary breeders provide shade and restrict access by predators. They may also have reduced densities of parasites, although this was not measured. When the schooling Sardine was plentiful, colonial breeding may have facilitated sharing of information on its distribution and group foraging.

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