

## FACTORS INFLUENCING GROWTH OF THE AFRICAN PENGUIN COLONY AT BOULDERS, SOUTH AFRICA, 1985–1999

R. J. M. CRAWFORD\*, L. J. SHANNON\*, P. A. WHITTINGTON† and G. MURISON‡

This paper reports on growth of the Boulders colony of African penguins *Spheniscus demersus* from inception in 1985 to the present. More than 900 pairs now breed there. Growth of the colony slowed in 1995 and 1996 and reversed in 1998, coinciding with periods of low abundance of Cape anchovy *Engraulis capensis* off South Africa. In December 1996, penguins were excluded from a portion of land where they had formerly bred. They responded by increasing the density of their nests in other areas and expanding their area of breeding longshore. These patterns indicate that food and not space are currently controlling colony growth rate. Much of the colony growth probably results from immigration of first-time breeders from other colonies. Of immigrants, 70–80% may be from Dyer Island to the south-east, where numbers of penguins have decreased. Boulders also is frequently visited by penguins from other colonies, and by rehabilitated birds.

African penguins *Spheniscus demersus* colonized Boulders, near Simonstown, in 1985 (Cooper 1985). It was one of three colonies of African penguins formed in South Africa's Western Cape between 1982 and 1985. The others were Stony Point at Betty's Bay in 1982 (Broni 1982) and Robben Island in Table Bay in 1983 (Crawford *et al.* 1995a). The subsequent histories of the colonies at Stony Point and Robben Island have been described by Whittington *et al.* (1996) and Crawford *et al.* (1995a, 1999) respectively. In this paper, the growth of the penguin colony at Boulders during its first 15 years, from 1985–1999, is described. Factors that may have influenced the numbers of penguins moulting and breeding at Boulders, the region occupied by breeding birds, and the origin of birds breeding there are discussed.

The earliest mention of penguins on land in the vicinity of Simonstown comes from Governor Simon van der Stel on 19 November 1687, who mentions a rock where "there were many penguins and gulls which were so tame they could be caught by hand" (McKenzie 1998). From the description of the rock, Becker (1987) is of the opinion that van der Stel was referring to a rock known as "Noah's Ark", a well-known landmark in Simons Bay, which obtained its name from its peculiar shape.

## METHODS

### Counts and nest maps

Counts were made at Boulders of African penguins that were in the feather-shedding phase of moult.

These counts were undertaken every two weeks during the main period of moult, from October to March, commencing in 1992/93. African penguins moult annually, and on average the feather-shedding phase takes 12.7 days (Randall *et al.* 1986). Therefore, counts at intervals of two weeks are of different individuals, and may be summed to obtain an estimate of the overall number of birds at a colony (Randall *et al.* 1986). Separate counts were made of birds in adult and immature plumages, except in 1999/2000, when personnel of South African National Parks counted the two categories together. On each of three counts undertaken by personnel of Marine & Coastal Management (MCM) on 15 October 1999, 1 November 1999 and 6 January 2000, the ratio of adults to immature birds for individuals shedding feathers was 10:1. This ratio was used to assign counts by personnel of South African National Parks to maturity categories for October 1999 to January 2000. For February and March 2000, when relatively more immature birds moult (Underhill and Crawford 1999), a ratio of 3 adults: 2 immature birds was used to assign birds to categories, based on a count at Boulders undertaken by MCM on 1 March 2000. A total of 96 counts was made in the eight moult seasons, an average of 12 per season.

At Robben Island, <5% of penguins in adult plumage and <7.5% of those in immature plumage moult between April and September (Underhill and Crawford 1999). Ten counts at Boulders showed that the numbers moulting there between April and September were similarly small and would have little impact on the estimate of penguins moulting at the colony. Therefore, counts of birds shedding feathers in summer were assumed to represent the numbers alive in the previous

\* Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa. E-mail: crawford@sfri.wcape.gov.za

† Avian Demography Unit, University of Cape Town, Rondebosch 7700, South Africa

‡ Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa

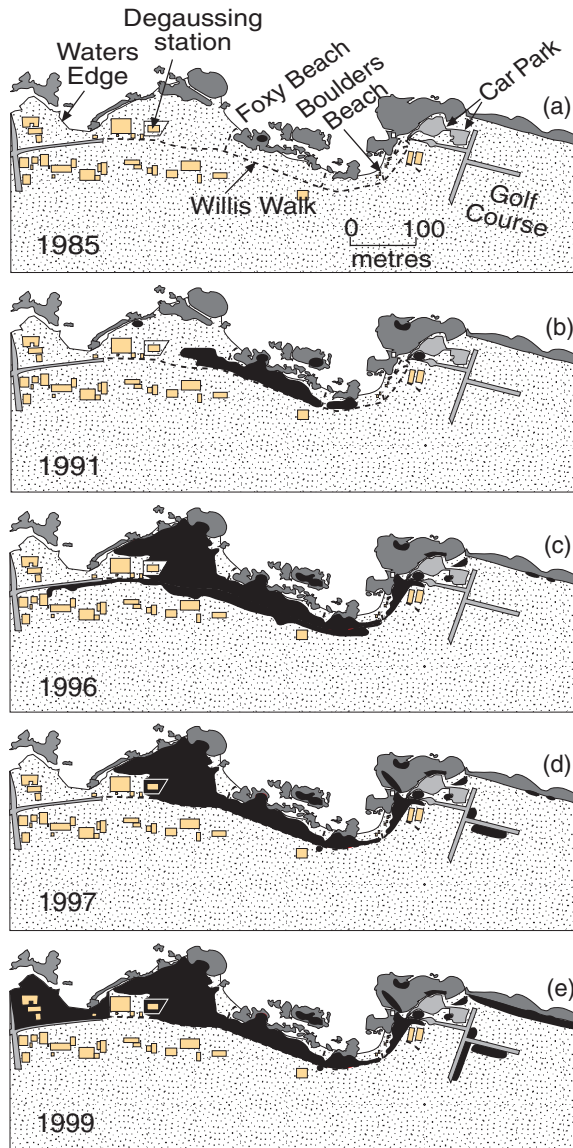


Fig. 1: The distribution of penguins at Boulders showing the extent of areas occupied by breeders (shown in black) in (a) 1985, (b) 1991, (c) 1996, (d) 1997 and (e) 1999

breeding season.

Counts of the number of active nests of penguins at Boulders were made each year between 1985 and 1999. Counts up until 1994 have been summarized by Crawford *et al.* (1995b). Between 1982 and 1999, a total of 37 counts was made, ranging from one to eight per year. They were conducted between March

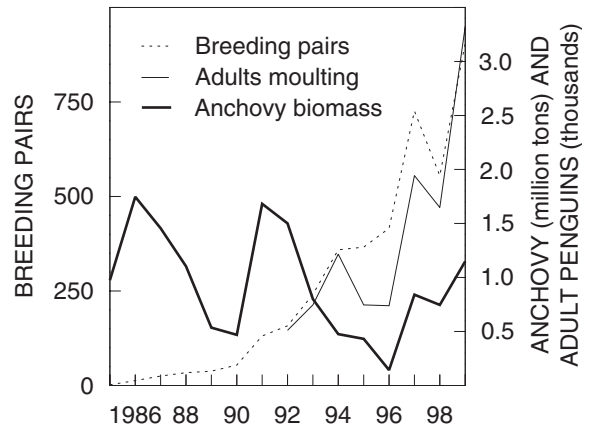


Fig. 2: Trends in the maximum number of breeding pairs of African penguins at Boulders, in the number of adults that moulted there, and in the spawner biomass of anchovy off South Africa, 1985–1999

and October, which spans the main breeding period of penguins in the Western Cape (Crawford *et al.* 1995a, b). The highest count of active nests in a year was used as an index of the breeding population in that year.

The distributions of nests of African penguins were mapped in 1985, 1991, 1996, 1997 and 1999. A fence was constructed on the seaward boundary of Willis Walk, a path that runs inshore of the coast (Fig. 1), in November and December 1996. Gates in this fence were closed on 4 December 1996 to restrict penguins to the seaward side of it.

### Food abundance

The relationships between spawner biomass of Cape anchovy *Engraulis capensis* and the South African sardine *Sardinops sagax* and numbers of penguins nesting or moulting at Boulders were investigated. Anchovy and sardine are the most important food items of African penguins off the west coast of South Africa (Davies 1955, 1956, Rand 1960, Duffy *et al.* 1985, Wilson 1985, Adams *et al.* 1992, Crawford and Dyer 1995, Crawford *et al.* 1995a). Estimates of spawner biomass off South Africa for these two fish species are available from 1985 to 1999 (Hampton 1987, 1992, 1996, Barange *et al.* 1999, MCM unpublished data). Numbers of penguins breeding at Boulders were modelled using the equation:

$$N_t = aN_{t-1} + bA_t \quad ,$$

where  $a$  and  $b$  are constants,  $N_t$  the number of pairs

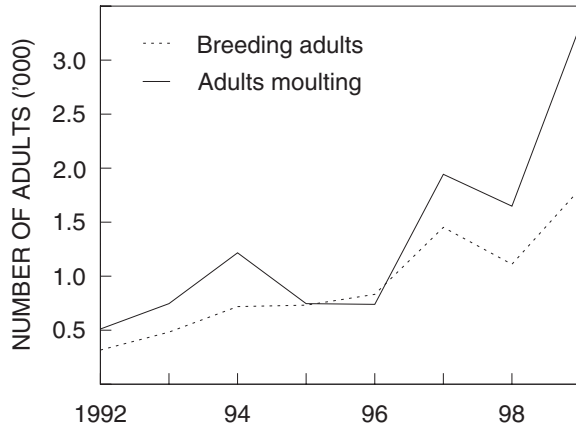


Fig. 3: Estimates of the number of African penguins that bred at Boulders compared with the number of birds in adult plumage that moulted in the following summer, 1992–1999

breeding in year  $t$  and  $A_t$  is the spawner biomass of anchovy in year  $t$ .

#### Nesting success and inter-colony movements

Reproductive success of African penguins at Boulders was measured in 1998. Nests were marked during the first week of April. Additional nest sites were marked until mid July to increase overall sample size. Nest contents (number of eggs or chicks) were recorded at 10-day intervals. Monitoring continued to the end of August 1998. Mayfield's (1975) method was used to calculate nest success, defined as the probability of an egg producing a fledged chick. Chicks were considered successfully fledged if they attained final fledging plumage, i.e. an age of 60–80 days. Johnson's (1979) method was used to calculate variance.

In other years, breeding success was not measured at Boulders, but it was at Robben Island, on the opposite side of the Cape Peninsula, in terms of average number of chicks fledged per breeding pair (Crawford *et al.* 1999). This measure was used to explore how breeding success may influence subsequent recruitment to the breeding population.

The occurrence at Boulders of African penguins that had been banded elsewhere, and movements from Boulders of penguins banded there, were investigated using information collated by the Avian Demography Unit, University of Cape Town. The age at which birds of known age were first seen breeding was recorded. An analysis was made of those years when birds visited or first settled at Boulders. It ex-

cluded birds younger than three years, which usually do not breed (Crawford *et al.* 1999), and rehabilitated birds that were recorded at Boulders within two months of release and that may have been in transit to their "home" colonies.

## RESULTS

### Population trends

The numbers of active nests and of adult penguins moulting at Boulders increased from colonization in 1985 to the present (Fig. 2). The rate of increase of the breeding population slowed in 1995 and 1996, with the addition of only 65 nests in those two years. In 1998, there was a slight reversal in the growth.

Numbers of adults that moulted showed a similar trend, with a large increase between 1992 and 1999. A decrease in adults moulting in 1995 and 1996 coincided with a small increase in the breeding population; both measurements decreased in 1998 (Fig. 2). The number of active nests is significantly related to the number of adults that moulted the following summer ( $n = 8$ ,  $r = 0.912$ ,  $p < 0.001$ ). In 1995 and 1996, numbers of adult penguins breeding at Boulders (taken as twice the maximum nest count) were almost the same as the numbers of birds in adult plumage that moulted the following summer (Fig. 3). In other years, more birds moulted than were estimated to breed.

The decrease in growth rate in 1995 and 1996 and the reversal in 1998 corresponded with decreases in the abundance of anchovy in those years (Fig. 2). The number of active nests of penguins at Boulders was modelled by the equation

$$N_t = 1.13N_{t-1} + 37.29A_t \quad .$$

This model accounted for 78% of the variation in numbers of active nests recorded. Models relating the breeding population to the biomass of sardine and to the combined biomass of anchovy and sardine did not explain as large a proportion of the variation. Residuals obtained from the model that used only anchovy biomass, by subtracting model estimates from maximum counts, are shown in Figure 4. Residuals were small from 1986 until 1996, but attained large positive values in 1997 and 1999 and a large negative value in 1998. Also shown on Figure 4 is the average production of chicks per breeding pair at Robben Island three years earlier. There is correspondence between this measurement and model residuals of nest counts at Boulders, particularly for the period 1996–1999. Over the period 1992–1999, these two parameters are positively, but not significantly, correlated ( $n = 8$ ,  $r = 0.617$ ,  $p < 0.2$ ).

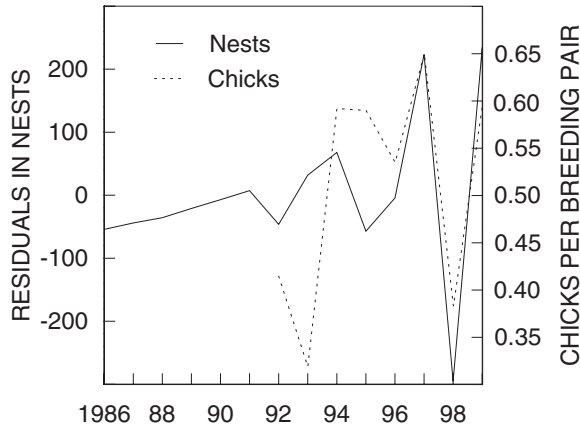


Fig. 4: Residuals generated by subtracting model estimates of nests of African penguins at Boulders from the maximum numbers counted, 1986–1999. Also shown is the mean number of chicks fledged by pairs of penguins at Robben Island three years earlier (from Crawford *et al.* 1999)

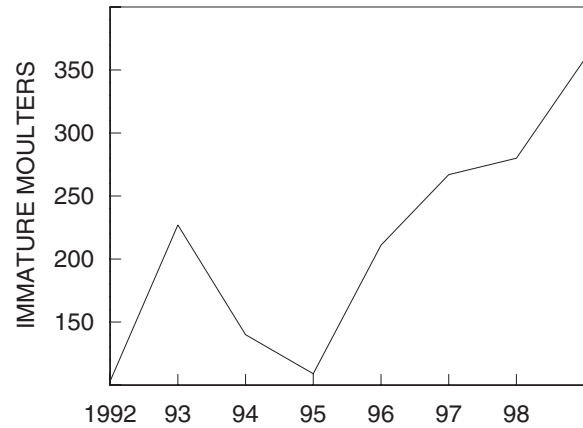


Fig. 5: Numbers of African penguins in immature plumage that moulted at Robben Island, 1992–1999

( $n = 513$  nests,  $SD = 0.12$ ). Pairs produced on average 0.61 fledglings per breeding attempt.

There was a noticeable decrease in the numbers of immature penguins that moulted at Boulders from 1993 to 1995. Otherwise, numbers have increased (Fig. 5).

### Nesting area and success

In 1985, penguins first nested on a rock between Foxy and Boulders beaches (Fig. 1). By 1991, the area of nesting had expanded north of Foxy Beach and south of Boulders Beach, but remained seawards of Willis Walk. By 1996, it had expanded farther north and south. Between 1992 and 1996, the number of nests adjacent to and north of Foxy Beach increased from 10 to 172. By 1996, there were also 101 nests on the landward side of Willis Walk. Following closing of gates in a fence along Willis Walk in December 1996, birds were no longer easily able to nest on the landward side of the path. Birds are assumed to have relocated to the seaward side of the path. The number of nests adjacent to and north of Foxy Beach increased from 172 in 1996 to 339 in 1997. It was 395 in 1999, when birds were also nesting in the vicinity of Waters Edge.

A total of 513 nests was monitored at Boulders in 1998. Of these, 92% were followed from the incubation stage and represented a total of 843 eggs. The average clutch size was 1.79 eggs ( $n = 471$  nests,  $SD = 0.04$ ). Overall, 34% of eggs laid produced fledged chicks

### Inter-colony movements

Until August 1999, there were 198 records of birds that moved to or from Boulders and other localities. Only 11 of these related to birds banded at Boulders

Table 1: Numbers of African penguins banded at other localities and later seen at Boulders

Colony where banded	Banding age			
	Adult	Chick (pre-fledging)	Juvenile (post-fledging)	Age unknown
Bird Island, Algoa Bay	1	10		1
Cape Recife <sup>1</sup>	2	35		
Dyer Island	3	5		
Seal Island, False Bay	1	7		
Robben Island	10	38		
SANCCOB <sup>2</sup>	16		7	2
Dassen Island		40		
Saldanha Bay islands		2		
Possession Island	1			
Ichaboe Island		5		
Mercury Island	1			
Total	35	142	7	3

<sup>1</sup> Rehabilitated bird originally stranded in KwaZulu-Natal

<sup>2</sup> Rehabilitated birds, most of which were released at Robben Island

Table II: Colonies of origin of birds banded as chicks and later recorded alive at Boulders. Numbers of those birds seen at Boulders when younger and older than two years are indicated

Colony of origin	Distance (km) and direction from Boulders	Number of chicks younger than 2 years seen at Boulders	Number of chicks older than 2 years seen at Boulders
Bird Island, Algoa Bay	725, East	6	2
Dyer Island	100, East	9	21
Stony Point	50, East	3	2
Seal Island, False Bay	17, East	3	3
Robben Island	90, North	22	16
Dassen Island	140, North	26	13
Saldanha Bay islands	190, North	2	
Ichaboe Island	1 000, North	1	4

being seen elsewhere, whereas 187 were banded or released at other colonies and subsequently sighted at Boulders (Table I).

All of the 16 birds in adult plumage banded by the Southern African National Foundation for the Conservation of Coastal Birds (SANCCOB) arrived via or continued on to other penguin colonies, some settling to breed. One had previously been recorded at Bird Island, Algoa Bay, after its release from Robben Island, whereas another had a week-old chick on Dyer Island prior to its being sighted at Boulders. Two other birds continued from Boulders to Bird Island, Lambert's Bay, and Dyer Island respectively. One oil-spill victim moulted at Boulders before continuing to Robben Island. Four other survivors from oil spills moved on to Dassen Island after visiting Boulders.

In all, 19 penguins were recorded at Boulders, having been banded in adult plumage at other breeding colonies. However, their true colony of origin remains uncertain because the breeding status of birds at banding is not always known or recorded on banding schedules. A bird banded at Bird Island, Algoa Bay, was found sick at Boulders five years and eight months

later, having been seen 10 days previously at Dyer Island. It subsequently died. Two were banded at Dyer Island, one subsequently breeding at Boulders. Three were banded at Stony Point, one later breeding at Boulders, one was banded at nearby Seal Island in False Bay, and 10 at Robben Island, one of which subsequently bred at Boulders. Two birds travelled from Namibia, one from Possession Island, c. 900 km away, and one from Mercury Island, a distance of c. 1 000 km.

Seven birds banded as juveniles (i.e. post-fledging in immature plumage) and later seen at Boulders were all birds that had been rehabilitated by SANCCOB, six having been oil-spill victims. One was breeding at Boulders, one had previously been seen at Bird Island, Algoa Bay, and one was subsequently recorded at Dyer Island. Three more were later seen at Dassen Island, one having been oiled for the second time at Boulders.

Perhaps the most interesting information comes from the birds banded as chicks, because their age and colony of origin are both known. A total of 142 chicks, banded at colonies other than Boulders, was subsequently recorded visiting or settling at the Boulders colony. Of these, 78 were younger than two years old when first recorded at Boulders. It is known that young African penguins range widely after fledging (Randall *et al.* 1987). Normally they will return to their natal colony prior to their first attempts to breed (Randall *et al.* 1987). Of these 78 chicks, six were dead when recorded at Boulders. Origins of the 72 that were seen alive are shown in Table II. A total of 21 came from colonies east of Boulders and 51 from colonies to the north. Of these birds less than two years old, 18 were later recorded back at their natal colonies, including one bird that returned to Ichaboe Island, Namibia; a round trip of almost 2 000 km (Table III). A chick that had been banded at Bird Island, Algoa Bay, was later recorded at Dassen Island and another, banded at Seal Island in False Bay, continued on to Stony Point. Of those banded at Dassen Island, two were later seen at Robben Island, one continued to Ichaboe Island and eight returned to

Table III: Fate of birds banded as chicks at other colonies and then recorded at Boulders

Age at sighting	Found dead	Found sick, injured or oiled	No subsequent sightings	Returned to natal colony	Settled at Boulders	Later seen at other colonies
Two years or younger when first seen at Boulders	6	4	42	18	2	6
Older than two years when first seen at Boulders	3	3	29	18	10	1
Total	9	7	71	36	12	7



Table IV: Details of the seven birds banded as chicks at other colonies that were later seen breeding at Boulders

Band number	Age at breeding	Natal colony
A1973	7 years 2 months	Dyer Island
S1466	7 years 2 months	Dassen Island
S5076	4 years 0 months	Dyer Island
S5407	6 years 1 month	Dyer Island
S10826	5 years 9 months	Dyer Island
S13492	5 years 9 months	Robben Island
S20493	3 years 6 months	Dyer Island

Dassen. Of the nine birds banded at Dyer Island, three were known to have returned there. Six of the 22 penguins banded at Robben Island returned there after appearing at Boulders, one was later recorded at Seal Island and one was subsequently found dead.

In addition, 64 birds banded as chicks were seen at Boulders when aged two years or older. Three were dead. Natal colonies of the 61 that were alive are shown in Table II. In all, 28 came from an easterly direction, whereas 33 arrived from colonies farther north. A total of 29 was not seen subsequently, but 18 were known to return to their natal colony (Table III), including three of those from Dyer Island and one from Stony Point. Of birds from Robben Island, eight were later seen back there, one having moulted at Boulders. Six of the Dassen birds later returned there and one of the Ichaboe birds seemed to be on its way back, being later reported both from Dassen Island and Bird Island, Lambert's Bay. Ten birds settled or appear to have settled at Boulders (Table III), in that they either bred there or were seen there on several occasions over the course of two or more years and were not known to return to their natal colonies.

Three birds of unknown age, two of which had been rehabilitated by SANCCOB, were later seen at Boulders (Table I). One of these, a breeding bird from Dyer Island, was found dead. The third bird, found stranded on a beach in Kwazulu-Natal and later released at Cape Recife in the Eastern Cape, was subsequently found injured at Boulders and taken to SANCCOB. It was later released again at the Boulders colony.

Of four birds banded as adults at Boulders, one moulted at Dassen Island, whereas three were seen at Robben Island, one of which was moulting. A chick from Boulders that had been hand-reared at SANCCOB was seen moulting at Dassen Island before returning to Boulders.

Seven chicks that fledged from other colonies were found breeding at Boulders (Table IV), and a further five may be settling there although they have not as yet

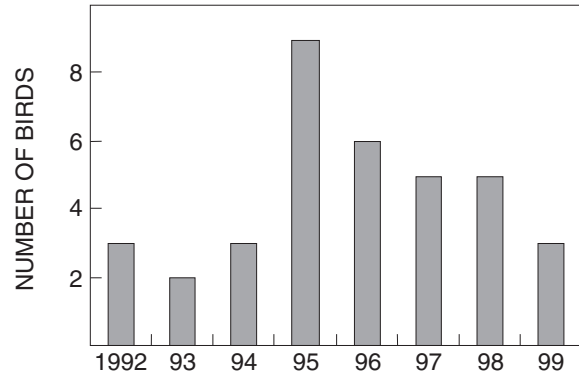


Fig. 6: Incidence of African penguins aged three years and older that had not recently been rehabilitated visiting Boulders, 1992–1999. Re-sighting effort increased substantially after mid 1994

been confirmed as breeders. The natal colonies of these 12 birds were Dyer Island (6), Stony Point (1), Seal Island (1), Robben Island (3) and Dassen Island (1).

Nine birds aged three years or older visited Boulders in 1995, more than in any other year (Fig. 6). Re-sighting effort of banded birds increased markedly from the second half of 1994 onwards, which explains the paucity of observations prior to 1995. Three birds appear to have settled at Boulders in both 1993 and 1998, with two birds settling there in each of 1995, 1997 and 1999 (Fig. 7).

## DISCUSSION

After Boulders was colonized by African penguins in 1985, the number of active nests increased each year, except in 1998. There was an almost linear increase up until 1990, despite a greatly reduced abundance of anchovy in 1989 and 1990 (Fig. 2). Thereafter, as anchovy increased in 1991 and 1992, there was a large increase in the number of nests. The breeding population continued to increase rapidly until 1994, but as anchovy biomass declined in 1995 and 1996, it stabilized. The number of adults moulting at Boulders decreased. Numbers of nests and of adults moulting and biomass of anchovy all increased in 1997, decreased in 1998 and increased again in 1999. These results suggest that expansion of the colony may have been limited by a scarcity of food in 1995, 1996 and 1998, when there were 366–621 pairs, but not in 1989 and 1990, when anchovy were similarly scarce but there were only 38–54 pairs (Crawford *et al.*

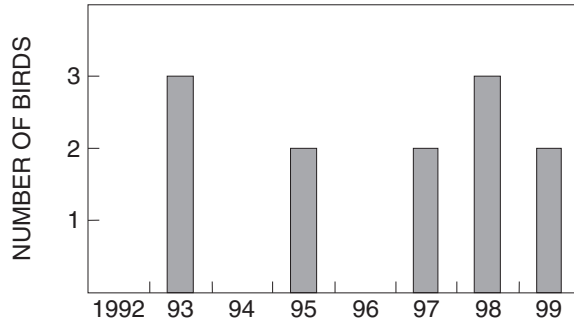


Fig. 7: Incidence of African penguins settling at Boulders, 1992–1999. Re-sighting effort increased substantially after mid 1994

1995b). From 1989 to 1995, both breeding success of adult penguins at and the estimated immigration of immature birds to Robben Island were significantly positively related to the biomass of anchovy (Crawford *et al.* 1999).

Although African penguins eat both anchovy and sardine, trends in numbers of penguins nesting and moulting at Boulders conform more closely with trends in the spawner biomass of anchovy than with trends in the biomass of sardine or of the combined biomass of these two fish species. The diet of penguins at Boulders has not been investigated, but at Robben Island anchovy formed the bulk of the food of penguins in the 1990s (Crawford and Dyer 1995).

At Possession Island, Namibia, the breeding population of African penguins decreased from an estimated 23 245 pairs in 1956 to just 327 in 1986 and then stabilized at a low level (Cordes *et al.* 1999). A scarcity of food was thought to be responsible for the very large decrease (Cordes *et al.* 1999). At Dyer Island, the penguin population decreased from 22 655 pairs in 1979 (Shelton *et al.* 1984) to between 2 000 and 3 000 pairs from 1997 to 1999, a decrease attributed to a reduced availability of anchovy to birds (Crawford 1999). Clearly, when colonies of African penguins attain high levels, colony size may be regulated by the availability of food in their vicinity.

It is noteworthy that, in 1995 and 1996, when anchovy attained its lowest measured level of abundance, the estimated numbers of adult penguins breeding at and moulting at Boulders were almost identical (Fig. 3). In other years, the number of birds in adult plumage that moulted at Boulders exceeded the estimated number of breeders. African penguins moult to adult plumage when approaching an age of two years (Randall 1989), but most do not breed until they are aged three years or older (Crawford *et*

*al.* 1999). Therefore, some birds in adult plumage may not be breeders. It is likely that such non-breeding birds account for the excess number of adults compared to breeders in certain years. These birds may be young adults from other colonies that are visiting Boulders, perhaps with intent to settle there. Crawford (1998) suggested that first-time breeders have flexibility to move from their natal colony to one where feeding conditions are favourable at the time. In 1995 and 1996, scarcity of anchovy seemingly made Boulders unattractive to prospective immigrants at the time when they were entering moult, although several birds aged three years or older visited (Fig. 6) and settled (Fig. 7) there in 1995.

Crawford *et al.* (1999) assumed that differences between numbers of adult penguins breeding and moulting at Robben Island reflected the proportion of mature birds that bred there. However, should pre-breeding birds in adult plumage visit colonies to moult, the proportion of birds estimated to breed using this method would be too low. This needs further investigation through observations of banded individuals.

Until 1999, space for breeding did not appear to limit the African penguin colony at Boulders, despite their being denied access to the area to the landward side of Willis Walk in December 1996. Most birds relocated their nests to the seaward side of this path, where densities of nests increased. In the vicinity of Foxy Beach, there were 0.9 nests·100 m<sup>-2</sup> in 1995, but 2.4 nests·100 m<sup>-2</sup> in 1997 (Ryan 1998). There was also longshore expansion of the colony. In sections of the Boulders penguin colony, densities of up to 7.5 nests·100 m<sup>-2</sup> have been measured (Ryan 1998). At St Croix Island in Algoa Bay, which has an area of 12 ha (Cooper and Berruti 1989), some 15 000 pairs of African penguin breed (MCM unpublished data), i.e. a density of 12.5 nests·100 m<sup>-2</sup>.

The relationship between residuals in the number of active nests at Boulders and breeding success at Robben Island three years earlier suggests that recruitment to the breeding population at Boulders may be influenced by the strengths of cohorts of first-time breeders produced in the Western Cape. At Robben Island, a few penguins attempted breeding when two years old, but most bred for the first time when aged between three and five years (Crawford *et al.* 1999).

The mean clutch size of 1.79 at Boulders in 1998 is slightly smaller than that recorded at Robben Island from 1989 to 1995 (1.86, range 1.81–1.92; Crawford *et al.* 1999). The mean number of chicks fledged per breeding attempt at Boulders in 1998 (0.61) lies towards the upper end of the range of 0.32–0.65 chicks fledged per breeding pair at Robben Island from 1989 to 1996 (Crawford *et al.* 1999, Fig. 4), but it is

similar to the value of 0.60 measured at Robben Island in 1998 (MCM unpublished data). Production at Robben Island was too low to account for the growth at that colony (Crawford *et al.* 1999), and this is likely to be the case at Boulders. Depending on values assumed for survival of adults and first-year birds, 59–87% of new adults at Robben Island during the period 1990–1995 were estimated to be immigrants (Crawford *et al.* 1999). If demographic parameters at Boulders are equivalent, a similarly high proportion of birds at Boulders will have hatched at other colonies.

The small sample of birds banded as chicks at other colonies, and later seen breeding at Boulders, suggests that 71% of immigrants may have come from Dyer Island (Table IV). The latter colony has declined by 90% since the mid 1980s, i.e. when the colony at Boulders was growing. It is thought that very few first-time breeders settled at Dyer Island in this period, most emigrating to other colonies (Crawford 1998). However, single birds that fledged at Robben and Dassen islands also recruited to the breeding colony at Boulders. The colony at Robben Island has been increasing since 1983 (Crawford *et al.* 1999). That at Dassen Island was relatively stable from 1991–1998, but it increased in 1999 (Crawford *et al.* 1995b, MCM unpublished data).

During the period 1985–1999, 2 688 chicks were banded at Dyer Island, 2 829 at Robben Island and 6 380 at Dassen Island (Crawford *et al.* 1999, A. C. Wolfaardt, Cape Nature Conservation pers. comm., and D. Oschadleus, South African Bird Ringing Unit pers. comm., PAW and MCM unpublished data). Therefore, the proportions of banded chicks from Dyer, Robben and Dassen islands, respectively, that settled to breed at Boulders are in the approximate ratio of 12:2:1. It appears that most of the breeders immigrating to Boulders are from Dyer Island, up to 80%. Similarly, at Robben Island (Crawford *et al.* 1999) and Stony Point (Whittington *et al.* 1996) most of the immigrant breeders are from Dyer Island.

The ages of chicks from other colonies that settled to breed at Boulders ranged from three to just over seven years. It is possible that the first attempt at breeding by some of these birds was missed, but none were known to have attempted breeding at their natal colony. Birds less than two years old recorded at Boulders were most likely transient, wandering individuals, whereas those aged three years and older were potential immigrants to the colony. The proportion of banded birds more than two years old seen at Boulders that had come from Dyer Island (34%) was higher than the proportion less than two years old from that colony (13%). The birds from Dyer Island appear less transient at Boulders than birds from

other colonies.

From sightings of banded birds, it is evident that Boulders forms an important “stopping off” point for wandering young birds and for rehabilitated birds following their release. Other movements of birds to the colony probably relate to birds coming in to forage. An adult fitted with a satellite transmitter in 1996, which had two large chicks in a nest at Dassen Island, spent a night at Boulders before returning to Dassen Island to feed its chicks (Crawford and Whittington 1997). Robben Island similarly is visited by penguins from other breeding localities (Crawford *et al.* 1995a).

African penguin chicks normally move in a westerly or northerly direction from their natal colonies. Of chicks from the Western Cape, 88% moved in a northerly direction (Randall *et al.* 1987). It is therefore interesting that, in the case of chicks that later arrived at Boulders, 49 (37%) were banded at colonies to the east and 84 (63%) at colonies to the north. Of birds banded as chicks and seen at Boulders when less than two years old, 29% were from colonies to the east (Table I). These proportions will be influenced by the greater numbers of chicks banded at colonies farther north than at colonies to the east.

#### ACKNOWLEDGEMENTS

We thank Ms L. Upfold and Mr B. M. Dyer (Marine & Coastal Management), Messrs P. J. M. Crawford and D. A. E. Crawford, and staff of South African National Parks (SANP) for undertaking counts of active nests and penguins in moult at Boulders, and B. M. Dyer for mapping the distributions of penguins breeding there. Dr P. J. Barham and Ms B. Barham (University of Bristol, UK) kindly made available their sightings of banded penguins. Ms I. Toerien (Simonstown Municipality) provided references on historical sightings of penguins in the Simonstown area. We are grateful to SANP for supporting the monitoring programme and to South African Bird Ringing Unit for supplying information on banded birds.

#### LITERATURE CITED

- ADAMS, N. J., SEDDON, P. J. and Y. M. VAN HEEZIK 1992 — Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment? In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 959–974.
- BARANGE, M., HAMPTON, I. and B. A. ROEL 1999 — Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, de-



- duced from acoustic surveys. *S. Afr. J. mar. Sci.* **21**: 367–391.
- BECKER, A. E. 1987 — *The History of False Bay up to 1995*. Simon's Town Historical Society: unpaginated.
- BRONI, S. C. 1982 — First recorded mainland breeding by the jackass penguin *Spheniscus demersus*. *Cormorant* **10**(2): p. 120.
- COOPER, J. 1985 — New breeding locality data for southern African seabirds. Jackass penguin *Spheniscus demersus*. *Cormorant* **13**(1): p. 81.
- COOPER, J. and A. BERRUTI 1989 — The conservation status of South Africa's continental and oceanic islands. In *Biotic Diversity in Southern Africa: Concepts and Conservation*. Huntley, B. J. (Ed.). Cape Town; Oxford University Press: 239–253.
- CORDES, I., CRAWFORD, R. J. M., WILLIAMS, A. J. and B. M. DYER 1999 — Decrease of African penguins at the Possession Island group, 1956–1995 – contrasting trends for colonial and solitary breeders. *Mar. Ornithol.* **27**: 117–126.
- CRAWFORD, R. J. M. 1998 — Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. *S. Afr. J. mar. Sci.* **19**: 355–364.
- CRAWFORD, R. J. M. 1999 — Seabird responses to long-term changes of prey resources off southern Africa. In *Proceedings of 22<sup>nd</sup> International Ornithological Congress, Durban, 1998*. Adams, N. J. and R. H. Slotow (Eds). Johannesburg; BirdLife South Africa: 688–705.
- CRAWFORD, R. J. M., BOONSTRA, H. G. v. D., DYER, B. M. and L. UPFOLD 1995a — Recolonization of Robben Island by African penguins, 1983–1992. In *The Penguins: Ecology and Management*. Daan, P., Norman, I. and P. Reilly (Eds). Chipping Norton, Australia; Surrey Beatty & Sons: 333–363.
- CRAWFORD, R. J. M. and B. M. DYER 1995 — Responses by four seabird species to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137**: 329–339.
- CRAWFORD, R. J. M., SHANNON, L. J. and P. A. WHITTINGTON 1999 — Population dynamics of the African penguin at Robben Island. *Mar. Ornithol.* **27**: 135–143.
- CRAWFORD, R. J. M., WILLIAMS, A. J., HOFMEYR, J. H., KLAGES, N. T. W., RANDALL, R. M., COOPER, J., DYER, B. M. and Y. CHESSELET 1995b — Trends of African penguin *Spheniscus demersus* populations in the 20th century. *S. Afr. J. mar. Sci.* **16**: 101–118.
- CRAWFORD, R. J. M. and P. A. WHITTINGTON 1997 — Jackass penguin. In *Southern African Bird Atlas. 1. Non-passerines*. Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V. and C. J. Brown (Eds). Johannesburg; BirdLife South Africa: 4–5.
- DAVIES, D. H. 1955 — The South African pilchard (*Sardinops ocellata*). Bird predators, 1953–4. *Investl Rep. Div. Fish. S. Afr.* **18**: 32 pp.
- DAVIES, D. H. 1956 — The South African pilchard (*Sardinops ocellata*) and maasbanker (*Trachurus trachurus*). Bird predators, 1954–55. *Investl Rep. Div. Fish. S. Afr.* **23**: 40 pp.
- DUFFY, D. C., WILSON, R. P. and A. BERRUTI 1985 — Anchovy in the diets of Dyer Island penguins: toward a test of two models of anchovy distribution. *S. Afr. J. Sci.* **81**(9): 552–554.
- HAMPTON, I. 1987 — Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 901–917.
- HAMPTON, I. 1992 — The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 1031–1050.
- HAMPTON, I. 1996 — Acoustic and egg-production estimates of South African anchovy biomass over a decade: comparisons, accuracy and utility. *ICES J. mar. Sci.* **53**: 493–500.
- JOHNSON, D. H. 1979 — Estimating nest success: the Mayfield method and an alternative. *Auk* **96**: 651–661.
- MAYFIELD, H. F. 1975 — Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- McKENZIE, R. 1998 — Penguins, fertiliser, or 3:2:1 zero. *The Cape Journal*. Cape Town, September 1998: 8–11.
- RAND, R. W. 1960 — The biology of guano-producing sea-birds. The distribution, abundance and feeding habits of the Cape penguin, *Spheniscus demersus*, off the south-western coast of the Cape Province. *Investl Rep. Div. Fish. S. Afr.* **41**: 28 pp.
- RANDALL, R. M. 1989 — Jackass penguins. In *Oceans of Life off Southern Africa*. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 244–256.
- RANDALL, R. M., RANDALL, B. M., COOPER, J. and P. G. H. FROST 1986 — A new census method for penguins tested on jackass penguins *Spheniscus demersus*. *Ostrich* **57**: 211–215.
- RANDALL, R. M., RANDALL, B. M., COOPER, J., LA COCK, G. D. and G. J. B. ROSS 1987 — Jackass penguin *Spheniscus demersus* movements, inter-island visits, and settlement. *J. Fld Orn.* **58**(4): 445–455.
- RYAN, P. G. 1998 — *African Penguins at Boulders Coastal Park, Simon's Town: the Scientific Basis for Management Options*. Cape Town; Percy FitzPatrick Institute of African Ornithology: 72 pp.
- SHELTON, P. A., CRAWFORD, R. J. M., COOPER, J. and R. K. BROOKE 1984 — Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. *S. Afr. J. mar. Sci.* **2**: 217–257.
- UNDERHILL, L. G. and R. J. M. CRAWFORD 1999 — Season of moult of African penguins at Robben Island, South Africa, and its variation, 1988–1998. *S. Afr. J. mar. Sci.* **21**: 437–441.
- WHITTINGTON, P. A., HOFMEYR, J. H. and J. COOPER 1996 — Establishment, growth and conservation of a mainland colony of jackass penguins *Spheniscus demersus* at Stony Point, Betty's Bay, South Africa. *Ostrich* **67**: 144–150.
- WILSON, R. P. 1985 — Seasonality in diet and breeding success of the jackass penguin *Spheniscus demersus*. *J. Orn., Lpz.* **126**: 53–62.