

POPULATION AND BREEDING OF THE GENTOO PENGUIN *PYGOSCELIS PAPUA* AT MARION ISLAND, 1994/95–2002/03

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The numbers of gentoo penguins *Pygoscelis papua* breeding at subantarctic Marion Island fell by 40% from 1994/95 to 2002/03, from 1 352 pairs to 806 pairs. Apart from a slight increase in 1998/99, there was a steady decrease in numbers breeding between 1995/96 and 2000/01, when the population stabilized. There is indication that in some years not all breeders nested and that some birds relocated to another colony after disturbance. From first clutches, pairs on average fledged between 0.01 chicks in 1997/98 and 0.58 chicks in 2002/03 (mean 0.38 ± 0.21). In 1994/95, replacement clutches increased the overall production of fledged chicks by 11%. Based on demographic parameters measured at other localities, the production of chicks at Marion Island was inadequate to maintain the population during the period 1995/96–2000/01. Consistency in trends in breeding success at five colonies suggests that factors operating at a mesoscale, rather than those specific to particular colonies, often influenced breeding success. Laying was later than normal in 1997/98, when there was almost total breeding failure with large losses of eggs and small chicks to returning Subantarctic skuas *Catharacta antarctica*. Future research on this Near Threatened species at Marion Island must take full account of its susceptibility to human disturbance.

Key words: breeding success, gentoo penguin, Marion Island, population trend, *Pygoscelis papua*, Subantarctic

The gentoo penguin *Pygoscelis papua* is one of four species of penguin that breeds at the Prince Edward Islands, including Marion Island, in the southern Indian Ocean. It has a circumpolar distribution, breeding between 46 and 66°S at subantarctic islands and on the Antarctic Peninsula (Marchant and Higgins 1990). The world population is of the order of 317 000 pairs (Ellis *et al.* 1998). The Crozet and Prince Edward islands are the northernmost breeding localities for the species (Woehler 1993). Gentoo penguins breed in several distinct colonies at Marion Island, most colonies being located in the eastern portion of the island (Adams and Wilson 1987, Fig. 1).

From 1994/95–2002/03, counts were undertaken of the numbers of gentoo penguins breeding at Marion Island to assess trends in the population there, as part of South Africa's contribution to the CCAMLR Ecosystem Monitoring Program (CEMP) of the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 1995). The species is regarded as Near Threatened in South Africa (Barnes 2000) and internationally (BirdLife International 2000). Also from 1994/95 to 2002/03, breeding success was measured at five colonies and information was obtained on the timing of breeding and on the mass of chicks at

fledging, following CEMP protocols. This paper reports results and considers factors that may have influenced trends in the population.

MATERIAL AND METHODS

Population

Counts of active nests and of unoccupied, recently constructed nests of gentoo penguins were undertaken at least once during July and August in every year between 1994/95 and 2002/03 for each colony at Marion Island (290 km²; 46°52'S, 37°51'E). Egg laying at Marion Island commences in June, with most first clutches initiated in July (Williams 1980a). Active nests were defined as those with either an adult or a chick present. In years when more than one count was undertaken in July and August, the highest count obtained at a colony was used as an estimate of the breeding population at that colony. This makes the assumption that birds did not nest at more than one colony in July and August of the same year.

During the period 1995/96–2000/01 at each of five

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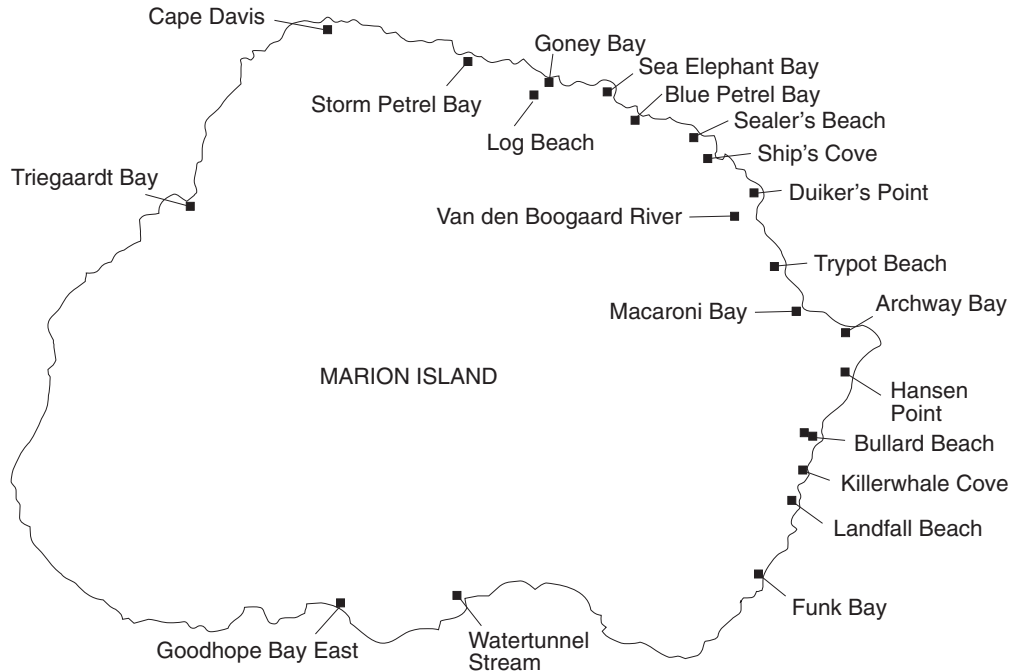


Fig. 1: The locations of breeding colonies of gentoo penguins at Marion Island, 1994/95–2002/03

colonies, the numbers of occupied nests were counted three times on the same day in order to estimate the error of counts. The relationship between the standard deviation (*SD*) of counts and size of the colonies counted was established, and used to calculate the coefficient of variation (*CV*) on counts of the overall breeding population of gentoo penguins at Marion Island.

Counts of nests during surveys were undertaken at any time of the day. The influence of this on the count of active nests was investigated by conducting counts at 08:00, 10:00, 12:00, 14:00 and 16:00 at the Van den Boogaard River colony on 15 July 1994 and at the Trypot Beach colony on 15 July 1995, 30 July 1996, 3 July 1998, 25 July 1998 and 16 July 1999.

Breeding

In all years between 1994/95 and 2002/03, the mean number of chicks fledged per breeding pair was estimated for the colonies at Trypot Beach, Macaroni Bay, Archway Bay, Hansen Point and Duiker's Point (Fig. 1), except at Duiker's Point in 1995/96. The number of

active nests at these colonies varied between 9 and 197. Colonies were visited every two weeks between 1 July and 15 September, and then weekly until 15 October. The numbers of active nests and of chicks in crèches were counted three times on most visits, and the means obtained. The maximum average number of active nests recorded on a single visit to a colony in a particular year was assumed to represent the number of breeding pairs at that colony, and the maximum average number of crèched chicks to represent the number of chicks that fledged from the colony, after subtraction of the number of crèched chicks known to have died.

Gentoo penguins may replace lost clutches 66 days later (Williams 1980a, Marchant and Higgins 1990). Replacement clutches were not taken into account in determining chick production per breeding pair, but were monitored at Trypot Beach in 1994/95.

From 1994/95 to 2001/02, the breeding chronology of gentoo penguins was studied by monitoring the progress of up to 50 nests at Trypot Beach, using CEMP protocols (SC-CAMLR 1995). The positions of nests within colonies were mapped, so that the progress of individual nests could be followed. In

2002/03, only the dates at which chicks entered crèches were recorded.

Trypot Beach was visited daily from 1 June until 50 nests had eggs or, if fewer than 50 pairs bred, all breeders had eggs. In this period, the arrival of adults at the colony was monitored in all years except 1994/95, 2000/01 and 2002/03. As adults were not banded, the number arriving on a given day was taken to be the difference between the numbers seen at the colony on that day and on the previous day. Because some birds may depart for sea, this may have underestimated numbers returning in the early stages of site establishment. At Marion Island, gentoo penguins moult in January and early February and by March and April have returned to breeding areas (Rand 1954). In some years, they are later absent again from breeding areas for only a few days, so that the dates of their return to colonies to breed are not well defined.

Once all breeders, or those at 50 nests, had eggs, nests were examined at two-day intervals until 48 days after the first egg was judged to have been laid, and then again on a daily basis until chicks had entered a crèche. Birds at Marion Island have a maximum clutch of two eggs (Williams 1980a). Eggs are laid at intervals of 3–5 days – a mean of 3.4 days was reported for Marion Island (Van Zinderen Bakker 1971) – and incubated for a period of 35–36 days (Marchant and Higgins 1990). The day when each of the chicks was first seen was recorded, as well as dates when chicks entered crèches (except in 2001).

In 1994/95, all nests were checked on each visit and the numbers of adults, eggs and chicks present at each nest were recorded, as well as the numbers of chicks in crèches. However, the checking of individual nests caused considerable disturbance (see also Williams 1980a). Therefore, from 1995/96, nests were examined from a distance using binoculars. Prone adults were assumed to be incubating, although some may have been brooding small chicks, so that from 1995/96 to 2001/02 hatching may have taken place earlier than indicated.

Dates when chicks fledged were gauged from decreases in the numbers of chicks in crèches, after accounting for any observed mortality of crèched chicks. Mortality of chicks from the start of the crèche stage to fledging at Marion Island ranges from 5% (van Zinderen Bakker 1971) to 28% (Williams 1980a). Chicks were not banded, and once they reached the crèche stage it was not always possible to distinguish those that originated from study nests from those hatched at other nests at Trypot Beach. The date when the first chick fledged was determined for three years, but the date when the last chick fledged only in 1994/95. The chronology of clutches that were assumed to be replacements (parents were not banded) was monitored

at Trypot Beach in 1994/95.

For each of the 1994/95–2002/03 breeding seasons, the mass at fledging of between 7 and 88 chicks (366 in total) was obtained. Weighing was undertaken from mid November onwards, after chicks had moved away from their nest sites towards the beach (SC-CAMLR 1995). In 1994/95, chicks weighed included those produced by replacement clutches.

RESULTS

Population

The time of day had little influence on the count of the number of active nests of gentoo penguins. At the Van den Boogaard River colony on 15 July 1994, five counts undertaken two-hourly between 08:00 and 16:00 varied between 33 and 35 active nests. At the Trypot colony, five counts conducted at these times on 15 July 1995 all gave 96 active nests. On 30 July 1996, counts varied between 68 and 72 active nests; on 3 July 1998 between 34 and 36 active nests; on 25 July 1998 between 69 and 71 active nests; and on 16 July 1999 between 37 and 39 active nests. When there was variation in the counts, maxima were obtained at any time between 08:00 and 16:00. Therefore, counts undertaken on surveys were not modified to account for the time of day when they were conducted.

During the period 1995/96–2000/01, CVs for counts at five colonies, where the mean number of occupied nests varied between 9 and 162, ranged from 0.0 to 3.2%. The SD of counts was significantly related to the size of colonies ($SD = 0.010 \times \text{colony size}$, $n = 23$, $r = 0.607$, $p < 0.005$). This resulted in a CV of about 1% for the counts of the overall breeding population in all years.

The number of gentoo penguin pairs breeding at Marion Island was about 1 350 in 1994/95, and 1995/96, then decreased by 40% to about 800 in 2000/01 and 2002/03 (Fig. 2). Between 1994/95 and 2002/03, numbers decreased at all colonies, except at Goodhope Bay (east) and Triegaardt Bay, on the western part of the island, and Goney Bay on the north coast (Fig. 1). The colony at Van den Boogaard River numbered 35 pairs in 1994/95, but was not subsequently used by gentoo penguins (Table I). In 2001/02, a new colony of 24 pairs formed at Log Beach, near Goney Bay. This colony increased to 49 pairs in 2002/03. At Goney Bay, there were 42–64 pairs from 1994/95 to 2002/03, just two pairs in 2001/02, but 75 pairs in 2002/03. At Triegaardt Bay, two pairs bred in 1994/95, none in 1995/96 and 7–11 pairs from 1996/97 to 2002/03. Numbers counted at Goodhope Bay East fluctuated be-

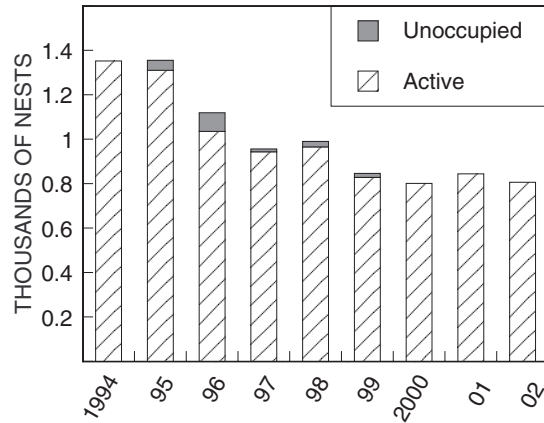


Fig. 2: Trends in the overall numbers of breeding pairs and of active nests counted at Marion Island between 1994/95 and 2002/03

tween seven and 17 pairs between 1994/95 and 2002/03. There were sometimes large fluctuations in the number of pairs recorded breeding at other colonies.

For example, at Bullard Beach there were 161 pairs in 1996/97, 114 in 1997/98 and 176 in 1998/99.

Breeding

For all colonies combined, the mean numbers of chicks fledged per pair from first clutches laid in a breeding season varied from 0.01 in 1997/98 to 0.58 in 2002/03 (Table II). When equal weight was given to each year's value, the overall mean number of chicks per pair fledged from first clutches was 0.38 ($SD = 0.21$, $n = 9$). From 1995/96 to 2001/02, pairs fledged on average 0.30 chicks per pair.

In 1994/95 at Trypot Beach, 16 replacement clutches produced a total of three fledged chicks. The 115 pairs at this colony raised 26 chicks to fledging from their initial clutches. Replacement laying resulted in the number of chicks fledged per breeding pair increasing by 11%, to 0.25 chicks per pair.

Trends in breeding success were often similar at the five intensively studied colonies (Fig. 3), with relatively poor breeding (<0.25 chicks per pair) at all colonies in 1994/95 (except Macaroni Bay), 1997/98 and 1999/00, and better breeding (>0.25 chicks per pair) at all colonies in 1995/96, 1996/97, 1998/99, 2000/01 (except

Table I: Maximum counts of active nests obtained during July and August at separate colonies of gentoo penguins at Marion Island, 1994/95–2002/03. Also shown are the numbers of unoccupied nests recorded in these months, numbers breeding at colonies in 1984/85 (from Adams and Wilson 1987) and the estimate of the overall breeding population

Colony	Maximum count									
	1984/85	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03
Trypot Beach	114	115	96	59	83	76	41	58	69	77
Macaroni Bay	15	21	28	15	17	13	10	10	10	9
Archway Bay	66	194	186	114	12	121	113	76	100	116
Hansen Point	55	58	63	56	41	42	23	29	34	38
Bullard Beach	66	201	171	161	114	176	142	166	174	77
Killerwhale Cove	18	9	4	5	7	11	7	5	4	1
Landfall Beach	42	45	51	32	32	37	28	20	28	16
Funk Bay	86	79	76	71	66	58	65	71	58	59
Watertunnel Stream	28	37	38	23	15	20	22	21	16	13
Goodhope Bay (east)	6	11	13	12	17	7	9	15	13	12
Triegaardt Bay	0	2	0	7	8	8	7	9	11	11
Cape Davis	55	47	44	36	39	33	31	25	26	19
Storm Petrel Bay	31	43	38	43	37	45	29	23	20	38
Log Beach	0	0	0	0	0	0	0	0	24	49
Goney Bay	46	62	61	61	64	42	42	64	2	75
Sea Elephant Bay	90	137	151	127	110	87	97	63	78	29
Blue Petrel Bay 15	48	48	48	39	40	28	27	28	29	
Sealer's Beach	42	49	47	35	22	34	30	17	24	26
Ship's Cove	71	101	141	89	79	96	71	67	86	73
Duiker's Point	29	58	54	41	31	19	33	35	39	39
Van den Boogaard River	13	35	0	0	0	0	0	0	0	0
Total active nests		1 352	1 310	1 035	943	965	828	801	844	806
Additional unoccupied nests		0	45	84	13	25	18	0	0	0
Overall population (pairs)	888	1 352	1 355	1 119	956	990	846	801	844	806

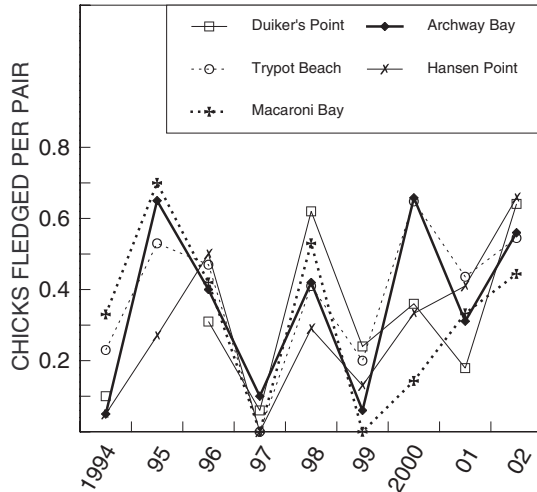


Fig. 3: Trends in the breeding success of five colonies of gentoo penguins at Marion Island, 1994/95–2002/03

Macaroni Bay), 2001/02 (except Duiker's Point) and 2002/03. In 1997/98, which was a particularly poor year, no chicks fledged at the colonies at Trypot Beach (83 pairs), Macaroni Bay (17 pairs) and Hansen Point (45 pairs). The highest mean number of chicks fledged per breeding pair at any colony was 0.70 at Macaroni Bay in 1995/96.

Adults began arriving at the colony at Trypot Beach between 1 and 26 June, depending on the year (Table III). In all years, the last adult had arrived by 23 July. Except in 1997/98 (20 July) and 2001/02 (1 June), the date when the first egg was presumed to have been laid was between 18 June and 11 July, a period of 23

days. In 1997/98, 95% of nests had eggs by 3 August, in 2001/02 by 14 June. In other years, this date varied between 12 and 25 July, a difference of 13 days. The earliest that an egg hatched was 16 July 2001. The date at which one-third of the eggs had hatched varied between 28 July and 30 August. Chicks began entering crèches between 28 August and 17 September and two-thirds of chicks were in crèches by between 2 and 24 September. Chicks began to fledge between 18 September and 6 October. In 1994/95, the last chick fledged on 29 December.

In 1994/95, replacement clutches were laid between 25 September and 5 October. From these, the first egg hatched on 30 October and the last on 9 November. The only three chicks to enter the post-guard stage had done so by 5 December.

The mean mass of chicks at fledging varied between 3.66 kg in the 1998/99 season and 5.66 kg in the 2000/01 season (Table II). However, in 1998/99 only seven fledglings were weighed. The minimum mass recorded for a fledged chick was 3.1 kg and the maximum 7.0 kg. The mean mass of the 366 fledged chicks weighed during the seasons 1994/95–2002/03 was 4.90 kg.

DISCUSSION

Population size and trend

Rand (1954) first estimated the number of gentoo penguins at Marion Island. He observed colonies of 50–100 birds each at 15 named (but only 10 mapped) localities on circumnavigating the island in summer 1951/52, which could be taken to represent of the order of 375–750 breeding pairs. However, Rand (1955), re-

Table II: Overall breeding success (i.e. chicks fledged per pair) and mean, maximum and minimum mass at fledging of chicks for gentoo penguins at Marion Island, 1994/95–2002/03. The sample sizes (n) and standard deviations (SD) of the means are indicated. For breeding success, n is the number of nests monitored and SD is the standard deviation of the means at five colonies (four colonies in 1995/96)

Season	Chicks fledged per pair			Mass at fledging (kg)				
	n	Mean	SD	n	Mean	SD	Maximum	Minimum
1994/95	466	0.12	0.12	88	4.45	0.45	5.40	3.40
1995/96	403	0.55	0.19	37	4.00	1.18	5.10	3.70
1996/97	357	0.42	0.07	57	4.79	0.70	6.25	3.25
1997/98	310	0.01	0.05	24	4.87	0.56	6.30	3.60
1998/99	319	0.42	0.13	7	3.66	0.51	4.50	3.10
1999/00	251	0.11	0.10	38	5.29	0.75	6.60	3.50
2000/01	232	0.51	0.22	50	5.66	0.57	6.70	4.50
2001/02	255	0.35	0.10	15	5.29	0.56	6.10	4.20
2002/03	279	0.58	0.09	50	5.52	0.60	7.00	4.50

Table III: Dates at various stages in the breeding cycle of gentoo penguins at Marion Island, 1994/95–2002/03 (1994/95 at Archway Bay, 1995/96–2002/03 at Trypot Beach)

Stage of breeding	Date								
	1994/95	1995/96	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2002/03
First adult at colony		26 Jun.	15 Jun.	14 Jun.	15 Jun.	4 Jun.		1 Jun.	
Median date of arrival		4 Jul.	28 Jun.	2 Jul.	24 Jun.	29 Jun.		10 Jun.	
Modal date of arrival		12 Jul.	11 Jul.	20 Jul.	24 Jun.	25 Jun.		1 Jun.	
Arrival of adults completed		12 Jul.	11 Jul.	20 Jul.	2 Jul.	23 Jul.		18 Jun.	
First egg laid	27 Jun.	2 Jul.	11 Jul.	20 Jul.	26 Jun.	18 Jun.	20 Jun.	1 Jun.	
Median laying date	11 Jul.	7 Jul.	22 Jul.	1 Aug.	13 Jul.	7 Jul.	6 Jul.	10 Jun.	
Modal laying date	1 Jul.	11 Jul.	11 Jul.	20 Jul.	30 Jun.	30 Jun.	7 Jul.	2 Jun.	
95% of nests with eggs	23 Jul.	12 Jul.	17 Jul.	3 Aug.	25 Jul.	24 Jul.	19 Jul.	14 Jun.	
Last egg laid	25 Jul.	12 Jul.	1 Aug.	13 Aug.	30 Jul.	27 Jul.	22 Jul.	18 Jun.	
First egg hatched	1 Aug.	21 Aug.	15 Aug.	18 Aug.	16 Aug.	4 Aug.	31 Jul.	16 Jul.	
One-third of eggs hatched*	7 Aug.	30 Aug.	21 Aug.	29 Aug.	21 Aug.	10 Aug.	18 Aug.	28 Jul.	
Median date of hatching	15 Aug.	1 Sep.	23 Aug.	28 Aug.	25 Aug.	16 Aug.	12 Aug.	28 Jul.	
Modal date of hatching	10 Aug.	30 Aug.	21 Aug.	31 Aug.	30 Aug.	25 Aug.	17 Aug.	1 Aug.	
Last egg hatched	28 Aug.	12 Sep.	30 Aug.	6 Sep.	5 Sep.	28 Aug.	25 Aug.	9 Aug.	
First chick crèching	30 Aug.	6 Sep.	15 Sep.	14 Sep.	13 Sep.	4 Sep.	17 Sep.		28 Aug.
Two-thirds of chicks crèching*	15 Sep.	21 Sep.	24 Sep.	14 Sep.	23 Sep.	18 Sep.	20 Sep.		2 Sep.
Median date of crèching	9 Sep.	17 Sep.	21 Sep.	16 Sep.	1 Oct.	11 Sep.	20 Sep.		31 Aug.
Modal date of crèching	8 Sep.	20 Sep.	18 Sep.	14 Sep.	23 Sep.	18 Sep.	20 Sep.		2 Sep.
Last chicks crèching	18 Sep.	27 Sep.	27 Sep.	18 Sep.	18 Oct.	18 Sep.	23 Sep.		2 Sep.
First date of fledging	18 Sep.	3 Oct.	6 Oct.						
Last date of fledging	29 Dec.								

*Dates when one-third of eggs had hatched and two-thirds of chicks were in crèches refer to eggs that hatched and chicks that entered crèches respectively

porting on what is assumed to be the same survey, refers to a total of 561 birds counted at only 13 named localities. Because the author was only present on Marion Island from October 1951 to April 1952 (Rand 1954), he would have missed the main peak of egg-laying in June and July (this study), so his count may reasonably be regarded as an underestimate of the then breeding population.

Van Zinderen Bakker (1971) considered the population of gentoo penguins at Marion Island in 1965/66 to be between 2 000 and 3 000 birds, mapping them at 18 colonies. He did not describe the method used to assess the population, but noted that it was "... difficult to estimate the number of non-breeding birds" (p. 252). Williams *et al.* (1975) gave the population at Marion Island in 1974 as 1 603. They did not indicate a unit but, as their estimate appeared in a table that also cites Van Zinderen Bakker's 1965/66 estimate of 2 000–3 000, it may be assumed to be of individual birds. Williams *et al.* (1975) also did not provide details of census methods, except to indicate that their count was undertaken between January and March and excluded Crawford and Triegaardt bays. Gentoo penguins were not reported at these two bays by Rand (1954, 1955), van Zinderen Bakker (1971) or Siegfried *et al.* (1978), or at Triegaardt Bay by Adams and Wilson (1987). In 1984/85, 28 pairs bred at Watertunnel Stream, at the extreme west of Crawford Bay (Adams

and Wilson 1987). From 1994/95 to 2002/03, Triegaardt Bay supported a maximum of 11 pairs and Watertunnel Stream a maximum of 38 pairs (Table I). Therefore, the exclusion of these bays by Williams *et al.* (1975) is unlikely to have substantially influenced their estimate. However, the main breeding season is completed by the end of December (Table III). Throughout the year, birds come ashore in the late afternoon, departing again to sea in the early morning (Van Zinderen Bakker 1971), so if birds had completed breeding by January–March, they may have been missed. The estimate of Williams *et al.* (1975) can be considered a lower limit, but cannot reasonably be compared with that of Van Zinderen Bakker (1971) for 1965/66. More information is provided by Siegfried *et al.* (1978) for the period 1974–1977. They report a total of 1 345 breeding pairs in at least 18 one-kilometre grid squares concentrated on the islands' eastern coast. Therefore, 18 may be considered the minimum number of colonies then present. Williams *et al.* (1979) cite a presumably rounded-off figure of 1 300 pairs for what is considered to represent the same survey.

Evidence exists for changes in the numbers and distribution of breeding colonies commencing within a few years of the occupation of Marion Island in January 1948. A breeding colony was present adjacent to the eponymously named Gentoo Lake, close to the meteorological station, in 1948 (photographed and de-

scribed by Bennetts 1948, Crawford 1952, 1982, 1999). However, by 1952 this colony had been permanently abandoned, almost certainly owing to disturbance caused by taking eggs for human consumption (Bennetts 1948, King 1952, 1954, Rand 1954). The first author noted that the gentoo penguins “soon leave their nest” on human approach and that the eggs “are very good eating”! Rand (1954) reported that “egging [was] indulged in to a great extent by some reliefs”.

Rand (1955) counted 15 birds ashore at Kaalkoppie on the west coast in summer 1951/52, a locality mapped as a breeding site in 1965/66 by van Zinderen Bakker (1971) and for the period 1974–1977 by Siegfried *et al.* (1978), who reported a colony of 35 pairs. By August 1984 this colony no longer existed, according to the mapped breeding distribution given by Adams and Wilson (1987). No records exist of birds ashore at Kaalkoppie subsequently. It is highly likely that a volcanic eruption and lava flow in 1980, which blocked access (with a cliff 6–12 m high) to a boulder beach previously used by southern elephant seals *Mirounga leonina* and gentoo and macaroni penguins *Eudyptes chrysolophus* at this locality (Verwoerd *et al.* 1981, Berruti 1982), made it no longer suitable for gentoo penguins to come ashore and to breed. Berruti (1982) reported no gentoo penguins present when visiting the locality in November 1980, an estimated 2–3 months after the irruption (Verwoerd *et al.* 1981).

Based variously on the small scales of published breeding distribution maps, the use of one-kilometre grids instead of named colonies, and the difficulty of identifying all the named breeding localities in the 1951/52 survey (Rand 1954, 1955, van Zinderen Bakker 1971, Siegfried *et al.* 1978, Adams and Wilson 1987), it is not considered sensible to be more precise about changes in the presence and distribution of breeding colonies of gentoo penguins at Marion Island prior to 1984/85.

In August 1984, there were 888 pairs of gentoo penguins at 24 colonies (some of which were at the same locality and therefore have been combined in Table I) at Marion Island (Adams and Wilson 1987), a decrease of some 450 pairs in about eight years since the period 1975–1977 (Siegfried *et al.* 1978). An observation was made during January 1981 of apparent predation of a gentoo penguin chick by a feral cat *Felis catus* (Berruti 1981). Penguin remains, unidentified to species, were found in 5–11% of cat stomachs during the periods 1974–1976, 1981–1983 and 1986–1989 (van Aarde 1980, van Rensburg 1985, Bloomer and Bester 1990). Van Rensburg (1985) reports a single gentoo penguin as the prey remains of a cat in the period 1981–1983. It is therefore possible, although it will remain unproven, that feral cats were responsible,

at least in part, for the population decline of gentoo penguins at Marion Island between the mid 1970s and mid 1980s. Cats were eradicated from the island in 1991 (Bester *et al.* 2002). Because gentoo penguins are primarily winter breeders at Marion Island, when burrowing petrels, the main avian prey of cats at the island, are largely absent (Cooper and Brown 1990), they may have been at some risk if cats had switched diets in winter. Gentoo penguin chicks have been recorded being killed by feral cats on sub-antarctic Macquarie Island (Garnett and Crowley 2000), but at a level not considered to have been a significant threat (Ellis *et al.* 1998). Jones (1984) reported that cats at Macquarie Island fed more on penguins during winter; 3% of scats contained penguin remains overall. Feral cats have been recorded preying on several other species of penguins, to a level to cause conservation concern in some cases (e.g. Berruti 1986, Darby and Seddon 1990, Stahel and Gales 1987, Ellis *et al.* 1998).

By 1994/95, the population had increased to the level observed in 1974–1977. Then, in five years between 1995/96 and 2000/01, it decreased by 554 pairs, from 1 355 pairs to 801 pairs (Table I). This is equivalent to a decrease of 8% per year. The low CV (about 1%) on the annual estimates of the overall population at Marion Island suggests a 95% probability of the population size falling within 2% of the estimate. At Bird Island, South Georgia, estimates also were considered accurate to 2% (Croxall and Rothery 1995).

The population estimated for Prince Edward Island, which is 21 km north-east of Marion Island, increased from about 200 pairs in 1976/77 (Williams *et al.* 1979) to 655 pairs in August 1984 (Adams and Wilson 1987), but then decreased to an estimated 475 pairs in 2001/02 (Ryan *et al.* 2003), again indicating substantial fluctuation.

It is of interest that the decrease in the number of gentoo penguins breeding at Marion Island between 1974–1977 and 1984/85 (about 450 pairs) and the increase at Prince Edward Island in the same period (also about 450 pairs) are so similar. At Bird Island, South Georgia immigration of gentoo penguins, especially first breeders, from the main island of South Georgia was considered likely. At Crozet Islands about 33% of first breeders breed at a locality other than their natal one (Croxall and Rothery 1995). At Bird Island, South Georgia, no birds banded as breeders were recorded breeding at another colony (Williams and Rodwell 1992). At South Shetland Islands, 90% of gentoo penguins reunited with their partner in the following year (Trivelpiece and Trivelpiece 1990). For the African penguin *Spheniscus demersus*, long-term emigration of first-time breeders to localities where feeding conditions are favourable at the time has

been reported but, because breeders show high fidelity to their mates, birds once breeding thereafter return to the same locality to breed (Crawford 1998, Crawford *et al.* 2001).

At Marion Island, it is probable that some gentoo penguins have moved between colonies. This appears to have taken place between Van den Boogaard River and Ship's Cove in 1995/96 and between Goney Bay and Log Beach in 2001/02 (Table I). The colony at Ship's Cove increased by 40 pairs between 1994/95 and 1995/96, approximately equivalent to the loss of the 35 pairs at Van den Boogaard River in the same period. Gentoo penguins at Van den Boogaard River were caught in 1994/95 to obtain diet samples. Disturbance brought about by such sampling may have caused birds to leave this locality in 1995/96 to join the colony at Ship's Cove, which is 1 km to the northwest (Fig. 1). Reasons for the formation of a colony at Log Beach in 2001/02 are not at this stage understood, although it should be noted that Rand (1954) reported a colony as present at this locality in 1951/52. These movements are inferred and were not shown by banding.

Several early observers and researchers reported that gentoo penguins at Marion Island are afraid of humans (e.g. Bennetts 1948, Crawford 1952, Van Zinderen Bakker 1971). They are also highly susceptible to human disturbance at subantarctic Heard Island (E. J. Woehler, Australian Antarctic Division, pers. comm.). Disturbance has caused Cape gannets *Morus capensis*, which normally show strong fidelity to breeding localities (Crawford *et al.* 1994, Klages 1994), to colonize new islands (Crawford *et al.* 1983). Apart from diet sampling and examination of nests of gentoo penguins in 1994/95, monitoring of gentoo penguins at Marion Island was not intrusive and disturbance is not considered to have caused the large decrease in numbers breeding there between 1995/96 and 2000/01.

Some other populations of gentoo penguins also have shown large fluctuations in numbers (Woehler and Croxall 1997, Woehler *et al.* 2001). For example, at Bird Island, South Georgia, the breeding population decreased by 75% between 1977 and 1979. It increased to half of its 1977 level in 1980 but decreased again from 1983 to 1984, from 1987 to 1988 and from 1990 to 1991, in between and in 1992 recovering to levels approximating that of 1980 (Croxall and Prince 1979, Williams 1990, Croxall and Rothery 1995). Superimposed on these short-term fluctuations was a longer-term decrease from the mid 1970s to the mid 1990s, as was also observed at King George Island (Woehler *et al.* 2001), more similar to the persistent downward trend at Marion Island from 1995/96 to

2000/01 (Fig. 2). At several localities on the Antarctic Peninsula there have been significant long-term increases in populations of gentoo penguins (Quintana and Cirelli 2000, Woehler *et al.* 2001). However, there have been large decreases at some island localities, including the Falkland Islands (Bingham 1998) and Bird Island, South Georgia (Woehler *et al.* 2001), which support about 75% of the total species' population (BirdLife International 2000).

Breeding

Fluctuations in the numbers of gentoo penguins breeding at specific colonies at Marion Island, for example at Bullard Beach between 1996/97 and 1998/99, suggest that, in some years, not all gentoo penguins breed. At Crozet Islands, only 84% of early breeders and 73% of late breeders bred in the following year (Bost and Jouventin 1990). Extensive non-breeding by adult birds has been shown for gentoo penguins and macaroni penguins at Bird Island, South Georgia, in some years (Williams and Rodwell 1992, Croxall and Rothery 1995).

In 1974/75 and 1976/77 at Marion Island, 17–60% of nests at different colonies (mean 43%) raised one chick to independence at an age of 60–90 days (Williams 1980a). This mean of 0.43 chicks fledged per pair falls within the range (0.01–0.58) recorded from first clutches between 1994/95 and 2002/03. There was an almost complete breeding failure at Marion Island in 1997/98, which was also observed for gentoo penguins at South Georgia in the 1977/78 and 1990/91 breeding seasons, when there was reduced availability of Antarctic krill *Euphausia superba* inshore for birds to feed on (Croxall and Prince 1979, Croxall and Rothery 1995).

In 1994/95, replacement clutches at Trypot Beach improved overall breeding success by 11%. At Crozet Islands, replacement clutches accounted for 15–20% of all clutches laid (Bost and Jouventin 1990). At Bird Island, South Georgia, six out of 203 pairs replaced clutches in 1988, but none did so in 1987 (Williams 1990).

Some gentoo penguins may breed at an age of two years (Croxall and Rothery 1995). However, the mean age at first breeding for male gentoo penguins is thought to be 3.5 years, the mean age at first breeding for all birds 3 years, adult survival 85% and survival of birds in their first and second years 80% in good years (Marchant and Higgins 1990, Trivelpiece and Trivelpiece 1990, Croxall and Davis 1999). If it is assumed that age at first breeding is three years and that all adults breed each year, it would be necessary for

pairs to fledge 0.55 chicks per year to maintain the population in equilibrium. This is greater than the overall mean of 0.38 chicks per pair per year from first clutches for the period 1994/95–2002/03 and more than the values recorded in 1994/95 and from 1996/97 to 2001/02 (Table II). If production is increased by 20% (to 0.46 chicks per pair) to allow for replacement clutches, it is still too low to achieve equilibrium with an age at first breeding of three years. For equilibrium with an age at first breeding of two years, it would be necessary for pairs to fledge on average 0.47 chicks per year. Given the likelihood that not all adults breed in each season (Croxall and Rothery 1995), production appears to have been inadequate to sustain the population at Marion Island, especially in 1994/95 and from 1995/96 to 2001/02.

Williams (1980a) and La Cock *et al.* (1984) note that breeding success of gentoo penguins is low at the Crozet and Prince Edward islands, at the northern extent of the species' breeding range. At Bird Island, South Georgia, gentoo penguins fledged 1.13 chicks per pair in the 1976/77 breeding season, about half of this in 1978/79 but none in 1977/78 (Croxall and Prince 1979), i.e. an average of about 0.56 chicks per pair per year. In five of 15 years at this locality, productivity was more than one chick per pair, there were two seasons of almost complete breeding failure and in the remaining eight seasons breeding success was from 0.59 to 0.94 chicks per pair (Croxall and Rothery 1995). At Cierva Point, Antarctic Peninsula, during 1992/93, 83% of pairs raised at least one chick to fledging (Quintana and Cirelli 2000). At the Falkland Islands, gentoo penguins fledged an average of 0.84 chicks per pair per year over a 12-year period (1990–2001, Bingham 2002). The lower production of chicks at northern than at southern breeding localities will require that, for populations to remain viable, other demographic parameters are more favourable at northern than at southern localities, e.g. that adult survival is higher or that birds breed at a younger age. Such parameters have not been measured at Marion Island.

The similarity in trends in breeding success at Marion Island at all five study colonies where this parameter was measured suggests that it is often influenced by factors operating at a mesoscale, e.g. over the foraging range of birds, rather than factors that are specific to individual colonies, as for example human disturbance that is restricted in nature. In 1984, 82% of all foraging trips of gentoo penguins at Marion Island were <40 km (Adams and Wilson 1987), indicating that birds feed near the island. There is also similarity in inter-season trends in breeding success of macaroni penguins at different colonies at Marion

Island (Cooper *et al.* 1997). Unlike the situation at Marion Island, there was no correlation between breeding success of gentoo penguins at different colonies at Bird Island, South Georgia (Williams 1990), although in years of substantially reduced availability of food there was pervasive poor breeding there (Croxall and Rothery 1995).

At Marion Island, the mass of chicks at fledging was not related to breeding success in the same year. For example, the heaviest chicks were weighed in the 1999/00 season, when breeding success was poor. This may result from the difficulty experienced by some field workers in catching chicks to weigh, without causing too much disturbance – e.g. in the 1998/99 season when breeding was reasonably successful but only seven chicks were weighed. Further, when food is scarce, chicks of low mass are more likely to die than when food is abundant, which may lead to a disproportionate number of heavy chicks surviving (Williams and Croxall 1990). Between 1994/95 and 2002/03, the mean mass at fledging varied from 3.66 to 5.66 kg (Table II), with an overall average of 4.9 kg, compared with 4.43 kg obtained by Williams (1980a) for three chicks in 1974/75 and 1976/77.

At the Crozet and Prince Edward islands, north of the Antarctic Polar Front, the laying period of gentoo penguins extends over five months, although more than 80% of pairs initiate laying within a period of three weeks. South of the Polar Front egg laying is more synchronous (Bost and Jouventin 1990). At Bird Island, South Georgia, 95% of clutches are initiated within a period of 14.5 days or less (Williams 1990). Laying is earliest at the northernmost breeding localities, and progressively later as one moves southwards (Williams 1980a).

At Marion Island, the reoccupation of nesting areas is gradual (Van Zinderen Bakker 1971). Egg laying has been reported in the first week of June (Crawford 1952). An egg was seen at Archway Bay on 7 June 1994 (ACW pers. obs.). However, egg laying normally commences between 16 and 25 June (Van Zinderen Bakker 1971, Williams 1980a) and peaks in late June or July. Relaying by failed breeders continues until early November (Adams and Wilson 1987). In 2001/02, egg laying at Marion Island was considerably earlier than usual, taking place from about 1 to 18 June. By contrast, laying was deferred in 1997/98 until about 20 July–30 August (Table III).

At the Crozet Islands, the date when the first egg was produced fell between 24 June and 15 July in four years. Peak laying varied by about a month between 21 and 25 July and 20 and 24 August (Bost and Jouventin 1990). In the present study, the date when the first egg was laid in the colony at Trypot Beach

was between 18 June and 11 July over six years. Except for 2001/02, the date at which 95% of nests had eggs was between 12 July and 3 August. Therefore, the variability in the onset of laying at the Crozet and Prince Edward islands is similar, but laying is usually initiated earlier at the Prince Edward Islands. At the Crozet Islands, the laying of replacement clutches commenced in early August and overlapped that of delayed first breeders (Bost and Jouventin 1990).

The timing of the more synchronous laying on South Georgia Island may vary by up to five weeks between years. Delayed breeding may result from a shortage of food in inshore waters or a severe preceding winter (Croxall and Prince 1979, Williams 1990, Croxall and Rothery 1995). It has been suggested that delayed laying at the Crozet Islands may result from food scarcity early in the breeding season (Bost and Jouventin 1990).

At Marion Island, the deferred laying in 1997/98 was associated with almost total breeding failure. Subantarctic skuas *Catharacta antarctica* returned to the island at the end of August (see also Williams 1980b) and inflicted substantial mortality on the eggs and small chicks of gentoo penguins (MDG pers. obs). Van Zinderen Bakker (1971) also noted that skuas preyed mainly upon nests of late-laying birds at Marion Island. Skuas *Catharacta* spp. are the main cause of mortality of both eggs and chicks of gentoo penguins at Cierva Point, Antarctic Peninsula (Quintana and Cirelli 2000).

The late breeding in 1997/98 coincided with a strong *El Niño* event that split year, which commenced in April and peaked in July/August (Wolter and Timlin 1998), when laying took place. For several seabirds at Marion Island, breeding was either exceptionally poor or unusually good in 1997/98. Poor breeding was experienced by species that forage close to the island, suggesting that availability of food was decreased for these birds (Crawford *et al.* 2003). *El Niño* events have also affected breeding by seabirds at other localities in the Southern Ocean (e.g. Croxall 1992, Chastel *et al.* 1993), including gentoo penguins (Croxall *et al.* 1988). Analysis of historical data on the abundance of seabirds off Peru and southern Africa indicated that, although their population dynamics are to a large extent influenced by local phenomena, linkages between these two regions are possible during extreme environmental conditions such as large *El Niño* events (Crawford and Jahncke 1999).

At Marion Island the gentoo penguin is protected from casual human disturbance by being placed in the highest protected management zone, with a 100-m perimeter around each breeding colony. Entrance is by way of a special permit issued for scientific and

conservation purposes only (Prince Edward Islands Management Plan Working Group 1996). This level of protection should continue in the intended revision of the management plan (Crawford and Cooper 2003). Any planned research activities on this Near Threatened species at Marion Island must be designed so as to reduce the effects of human disturbance on breeding success to the absolute minimum.

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A gentoo penguin at Marion Island (photo B. M. Dyer)