DECREASE IN NUMBERS OF THE EASTERN ROCKHOPPER PENGUIN EUDYPTES CHRYSOCOME FILHOLI AT MARION ISLAND, 1994/95–2002/03

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The number of eastern rockhopper penguins *Eudyptes chrysocome filholi* breeding at subantarctic Marion Island decreased from about 173 000 pairs in 1994/95 to about 67 000 pairs in 2001/02. During 1994/95–2002/03 pairs fledged on average 0.40 chicks per year, an amount thought insufficient to balance mortality of breeding adults, and there was a decrease in the mass at arrival at breeding colonies of both males and females. Except in 1997/98, the mass of chicks at fledging was less than that recorded at two other localities. These factors suggest an inade-quate supply of food for rockhopper penguins at Marion Island. Decreases of rockhopper penguins at several other localities also have been attributed to inadequate food. Rockhopper penguins at Marion Island continued to feed mainly on crustaceans during chick rearing. There was a marked increase in the contribution of fish to the diet in 1999/00 that coincided with an increase in mass at arrival at colonies of both males and females. Trends in numbers of pairs breeding in different sections of Marion Island were not always consistent, indicating the need for island-wide monitoring to establish the overall trend.

Key words: breeding success, diet, *Eudyptes chrysocome*, Marion Island, mass, population decrease, rockhopper penguin, Subantarctic

The rockhopper penguin *Eudyptes chrysocome* has a circumpolar distribution in the southern hemisphere, where it breeds at subantarctic and south temperate islands (Marchant and Higgins 1990). Three subspecies have been recognized, the southern *chrysocome*, northern *moseleyi* and eastern *filholi* forms. It is *filholi* that occurs at South Africa's Prince Edward Islands in the southern Indian Ocean, along with three other species of penguins. Eastern rockhopper penguins also breed at Crozet, Kerguelen, Heard, MacDonald, Macquarie, Campbell, Auckland and Antipodes islands, so their distribution extends from the south-western Indian Ocean to islands south of New Zealand (Ellis *et al.* 1998).

Woehler (1993) estimated the overall population of eastern rockhopper penguins to be at least 832 000 pairs. A decrease of 94% was reported for Campbell Island between the early 1940s and 1985 and attributed to rising sea surface temperatures causing euphausiids to move offshore, thereby affecting availability of prey to the penguins and the growth and survival of chicks (Moors 1986, Cunningham and Moors 1994). The population at Antipodes Islands is thought to have decreased between 1972/73 and 1989/90 and that at Auckland Island from 5 000–10 000 pairs in 1972/73 to 2 700–3 600 pairs in 1990 (Cooper 1992, Woehler and Croxall 1997, Ellis *et al.* 1998).

There have also been decreases in populations of other subspecies of rockhopper penguin. At Amsterdam Island in the south-western Indian Ocean, the population of northern rockhopper penguins decreased at a rate of 2.7% per year between 1971 and 1993. This decrease may have been caused by a drop in sea surface temperature affecting the distribution and abundance of prey organisms, or by a large increase in numbers of Subantarctic fur seals *Arctocephalus tropicalis* at the island (Guinard *et al.* 1998). At the Falkland Islands, the population of southern rockhopper penguins decreased by about 90% between 1932/33 and 1995/96 (Bingham 1998a).

At Marion Island in the Prince Edward Islands group, numbers of eastern rockhopper penguins breeding at three small study colonies decreased between 1983/84 and 1999/00 (Cooper *et al.* 1997, Woehler *et al.* 2001).

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Fig. 1: Marion Island, showing the sections of the coast where breeding pairs of rockhopper penguins were counted and the location (dots) of colonies monitored to estimate breeding success

This paper presents further evidence for reduced numbers of rockhopper penguins at Marion Island and considers reasons for the decrease.

MATERIAL AND METHODS

Population trend and breeding success

Counts of the number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and the Van den Boogaard River in north-eastern Marion Island (290 km²; 46°52′S, 37°51′E; Fig. 1) were made annually from 1983/84–2002/03 as close to 4 December as possible. At the same colonies, counts of the numbers of newlyhatched chicks and chicks in crèches were made as close as possible to 4 January and 28 February respectively (Cooper *et al.* 1997). These counts were undertaken from outside the colonies and are unlikely to have disturbed the breeding birds. From 1994/95 to 2002/03, each count was made three times and the mean and standard deviation calculated. For each season, the average number of chicks fledged per pair was calculated. Chicks in crèches were assumed to have fledged.

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From 21 November to 6 December 1994, from 13 November to 6 December 1996 and from 18 to 23 December 2001, all localities where rockhopper penguins breed at Marion Island were visited and the number of breeding pairs was counted or estimated. Counts at accessible colonies were made with the aid of binoculars and tally counters. Estimates were made for less accessible colonies by counting nesting birds in a visible section of the colony and multiplying by a factor to account for birds that probably could not be seen, for example in areas with cliff overhangs or in inaccessible lava tunnels that obscured birds. In 1996, the approximate error on counts and estimates was gauged from repeat counts and on-the-spot consideration of uncertainty of the area occupied by breeding birds. Because the count in 2001 was conducted 2-3 weeks later than in the other two years and hence breeding attempts by a greater proportion of pairs may have failed, the counts in 2001 were adjusted to account for failures between 7 December and the date of the survey using information collected at the three colonies where long-term monitoring is undertaken.

Counts were made of all active rockhopper penguin nests along two sections of the Marion Island coastline from 20 November to 17 December 1997, from 29 November to 15 December 1998, from 23 November to 8 December 1999, from 20 November to 7 December 2000 and from 28 November to 8 December 2002. The sections surveyed were Storm Petrel Bay to Hansen Point in the north-east of the island and Rook's Bay to Swartkop Point, but excluding Toffee Lava, in the southwest (Fig. 1). The sections were chosen because they were relatively easy to survey, so counts were thought more accurate than for other sections, and because they covered different parts of the island. In 1994, 1996 and 2001 these sections accounted for 25, 24 and 34% respectively of the overall count.

Timing of breeding

In 1994/95, the breeding phenology of rockhopper penguins was studied by monitoring the arrival of adults at Van den Boogaard River and Trypot Fault and the progress of 55 nests and the fledging of chicks at Trypot Hole. Methods used were those outlined by the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 1995). Because 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. The distributions of nests were mapped, so the progress of individual nests could be followed.

At Marion Island, adult rockhopper penguins reoccupy colonies during late October and early November. Laying takes place in late November and early December, and chicks hatch in late December and early January and fledge by mid March (Cooper and Brown 1990). The normal clutch of rockhopper penguins is two eggs (Williams 1980a). Averages at Marion Island for laying interval, incubation period of second-laid eggs and incubation period of first-laid eggs were 4.4, 34.2 and 39.1 days respectively (Williams 1981). Incubation does not commence until the second egg is laid and eggs are not warmed to steady temperatures until the second half of the incubation period (Burger and Williams 1979).

In 1994/95, the numbers of adults at Van den Boogaard River and Trypot Fault were counted daily from 20 October until 21 November. Nests at Trypot Hole were checked daily from 15 November until all chicks were in crèches. The days when each egg and chick was first seen were recorded, as well as days when chicks entered crèches. When all chicks were in crèches, their numbers were counted daily until fledging was complete. Records were kept of all chicks that died.

Mass of adults on arrival at colonies and of chicks at fledging

For each of the 1994/95–2002/03 breeding seasons, the mass at arrival at breeding colonies of 37–113 males and 40–102 females and the mass at fledging of 106–250 chicks was obtained. Males and females were weighed between 28 October and 14 November. Sexes were discriminated using bill measurements. Males are larger than females and have longer bills (Marchant and Higgins 1990). At Marion Island, mean culmen length for males is 45.7 mm (SD 1.4 mm) and for females 40.6 mm (SD 1.7 mm, Williams 1980b). Chicks that had obtained final fledging plumage were weighed in early March.

Diet

From 1994/95 to 2001/02, 30–45 stomach samples were collected each season between 6 January and 9 March, during the chick-rearing period (Cooper and Brown 1990). Birds were caught when they came ashore and their stomachs emptied using a stomach-flushing technique modified (water was poured down a tube rather than pumped into the stomach) from that described by Wilson (1984). Generally each bird's stomach was flushed only once. Samples were preserved in ethanol or frozen. In the laboratory, all liquid was drained from the sample through a small-meshed sieve. Each drained sample was then sorted into crustacean, cephalopod and fish components and then weighed to obtain their relative contribution to the diet.

The original biomass of cephalopods and fish ingested was not estimated. At Marion Island in 1984, the use of regressions relating lower rostral length of cephalopod beaks to length of dorsal mantle and mass increased the estimated contribution by mass of cephalopods from 2.5% (estimated from regurgitations) to 5%. Use of regressions relating otolith diameter to fish length and fish mass increased the estimated contribution by mass of fish from 6 to 14%. As a result the estimated contribution of crustaceans in the diet decreased from 91 to 81% (Brown and Klages 1987).



Fig. 2: Trends in numbers of rockhopper penguins breeding at three colonies at Marion Island and of these three colonies combined, 1983/84–2002/03 (updated from Cooper *et al.* 1997). The linear trend for the combined count is shown

RESULTS

Population trend and breeding success

The combined number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogaard River decreased in a fluctuating manner from 372 pairs in 1983/84 to 306 pairs in 1994/95 and to 129 pairs in 2001/02. It then increased to 244 pairs in 2002/03. The overall decrease between 1983/84 and 2002/03 was 34%, that between 1994/95 and 2002/03, 20%. Trends at the three colonies were similar (Fig. 2) and significantly related to each other. The strongest correlation was obtained between the nearby colonies of Trypot Hole and Trypot Fault (n = 20, r = 0.750, p < 0.7500.001). Correlations for the more distant colony at Van den Boogaard River with Trypot Hole (n = 20, r =0.700, p < 0.001) and Trypot Fault (n = 20, r = 0.505, p < 0.05) were weaker. The modelled rate of linear decrease of the combined number of pairs at the three colonies was 13 nests per year, i.e. 3.5% of the 1983/84 population. This trend was significant (n = 20, r =-0.803, p < 0.001). A least-squares model was used: $N_t = a - bt$, where a and b are constants and N_t the number of breeding pairs at time t, t = 0 being 1983.

The number of active nests at Trypot Hole, Trypot Fault and Van den Boogaard River combined decreased from 129 on 7 December 2001 to 70 between 10 and 14 January 2002, i.e. by 59 nests in 36 days. Assuming a linear decrease over this period, about 21 nests or 16% of the total would have been lost by December 20, the midpoint of the 2001/02 total island survey. There-

fore, the late total island count in 2001/02 was increased by 16%. The assumption of linear decrease may not be valid if nest failures occur at specific times in the breeding cycle.

Estimates of the overall population of rockhopper penguins at Marion Island decreased from about 173 000 pairs in 1994/95 to 67 000 pairs in 2001/02, i.e. by 61% (Table I). In 1996/97, the approximate error on counts was thought to be 5-20%, depending on the ease with which counts were undertaken. The highest errors were assumed for areas with dangerous cliff overhangs and inaccessible lava tunnels that obscured birds and for inaccessible beaches that were surveyed through binoculars. There was substantial variability on estimates for these regions, e.g. for Watertunnel Stream to Grey-headed Albatross Ridge. The estimated overall error on the 1996 count was 15%.

Estimates of the number of nests in the two sections of the island that were regularly counted decreased by 46%, from about 43 000 in 1994/95 to 23 000 in both 2001/02 and 2002/03 (Table I). This decrease was approximately linear, with the annual loss being about 5.6% of the total in 1994/95 (Fig. 3). The trend was significant (n = 8, r = -0.948, p < 0.001). From 1994/95 to 1997/98 counts decreased in both sections. From 1997/98 to 2002/03, the trends for the two sections were dissimilar. Numbers breeding between Storm Petrel Bay and Hansen Point decreased from 1997/98 to 1998/89 and again from 2000/01 to 2001/02, but were stable between 1998/99 and 2000/01 and increased in 2002/03. Conversely, numbers between Rook's Bay and Swartkop Point increased from 1997/98 to 1998/99 and from 2000/01 to 2001/02, but Table I: Counts of numbers of breeding pairs of rockhopper penguins for sections of the coast of Marion Island, 1987/88 and 1994/95–2002/03. Totals for regularly counted sections are indicated, as are the overall totals for years in which a complete count was conducted. For 2001/02 the count is shown, as well as an adjustment to account for failure of nests after 6 December, the date of completion of the 1994/95 and 1996/97. The adjustment was based on information collected at colonies that were monitored for breeding success (see text)

				Number	r of breedi	ng pairs				
Region	1987/88	1994/95	1996/97	1997/98	1998/99	1999/00	2000/01	2001/02	2001/02 adjusted	2002/03
Base to Trypot Fault	1 137	1 386	1 351	731	502	729	662	165	196	521
Irypot Fault to Macaroni Bay	350	293	2/4	261 200	× ×	84	8/ 2	0	0100	0.00
Macaroni Bay to Hansen Point	6 650	8 588	6 038	5 273	5 132	5 244	5 207	1 558	1 855	2 634
Hansen Point to Bullard Beach South	006	1 130	806					103	194	
Bullard Beach South to Sealer's Cove	5 100	11 640	8 072					2 281	2 715	
Sealer's Cove to Green Hill	2,960	5 392	5 535					1341	1 596	
Green Hill to Puisie	18 900	29 803	19 433					3 702	4 407	
Puisie to Watertunnel Stream	$20\ 000$	7 990	6 142					818	974	
Watertunnel Stream to Grey-headed Albatross Ridge	17 800	13 960	22 489					5 877	6 996	
Grev-headed Albatross Ridge to Rook's Bay	1 200	4 565	3 640					852	1 014	
Rook's Bay to La Grange Kop, excluding Toffee Lava	4 450	10 765	8 081	6719	9 615	7 022	6 925	9 594	11 421	6 422
Toffee Lava	2 000	8 774	10 357					4016	4 781	
La Grange Kop to Swartkop Point	3 300	6 645	5 694	6 344	8 399	6 531	6253	5038	5 998	6 305
Swartkop Point to Kaalkoppie	$4\ 800$	13 521	10 193					1 076	1 281	
Kaalkoppie to Kampkoppie	500	2446	1 827					1 476	1 757	
Kampkoppie to Mixed Pickle Cove	5 100	7 411	5 677					4 290	5 107	
Mixed Pickle Cove to Wild Cat Creek	$16\ 000$	15 977	13 633					5640	6714	
Wild Cat Creek to Storm Petrel Bay	5 530	7 632	6 008					5 382	6 407	
Storm Petrel Bay to Long Ridge (including Long Ridge)	9 950	5 329	5 028	6 122	5751	4688	4 977	203	242	4 530
Long Ridge to Ship's Cove	5650	6 309	5 570	5 236	4 055	4 201	4 463	1 563	1861	1 470
Ship's Cove to Base	5 375	3 521	4 118	3 535	2 518	3 007	2 551	963	1 146	1 302
Total for sections counted regularly	36 862	42 836	36 154	34 155	36 060	31 506	31 116	19 084	22 719	23 184
Total	137 652	173 077	150 118					55 998	66 664	

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BREEDING PAIRS (thousands)

40

35

30

25

20

2000

2002

CHICKS FLEDGED

(a)

100 100 100

(b)

10000 19971090

1994/05

0.45

HV 0.40 HV 0.35 HV 0.35 HV 0.30

0.25

3.50

3.30



- Overall

Selected sections

Linear (Selected sections)

decreased from 1998/99 to 2000/01 and in 2002/03.

From 1994/95 to 2002/03 the estimated mean number of chicks fledged by rockhopper penguin pairs, based on counts of incubating birds and of chicks in crèches at set times, varied between 0.35 and 0.46, except in 1998/99 (0.25), with an overall mean (weighting years equally) of 0.40 (n = 9, SD = 0.07, Fig. 4a).

Timing of breeding

In 1994/95, male rockhopper penguins began arriving at Trypot Fault on 29 October and at Van den Boogaard River on 30 October. Females were seen in these colonies for the first time on 2 November and 5 November respectively, i.e. 4-6 days after the first arrival of males.

Dates at various stages in the breeding of rockhopper penguins during the 1994/95 breeding season are shown in Table II. Egg-laying lasted from 17 November to 3 December and hatching from 25 December to 8 January. Chicks entered crèches between 19 and 29 January and fledged between 8 February and 14 March.

Mass of adults on arrival at colonies and of chicks at fledging

Between 1994/95 and 2002/03 there was a tendency for mass of both males and females on arrival at colonies to decrease (Fig. 4b). Mass on arrival of males was sig-



100000 1999/00

○ Female

Fig. 4: Trends at Marion Island for rockhopper penguins in (a) chicks fledged per pair, (b) mass on arrival at colonies to breed of males and females and (c) mass of chicks at fledging, 1994/95-2002/03

nificantly correlated with that of females (n = 9, r =0.752, p < 0.02). The average mass of birds on arrival at colonies (giving equal weight to both sexes) was related to trends in the combined number of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogaard River (n = 9, r = 0.725, p < 0.05) and to average breeding success at these colonies (n = 9, n = 1) $r = 0.660, p \approx 0.05$).

Mean mass of chicks at fledging was 1.39-1.77 kg from 1994/95 to 1996/97, in 1998/99 and in 2002/03, but from 1.90 to 2.13 kg in 1997/98 and from 1999/00 to 2001/02 (Fig. 4c).

2001/02

Male

2002103

200001

Linear (Female)

þ

199⁴

Table II:	Dates at various stages in the breeding of rockhopper
	penguins at Marion Island during the 1994/95 season

Stage of breeding	Date
First adult at colony	29 October
Median date of arrival of adults	9 November
Modal date of arrival of adults	9 November
Arrival of adults completed	20 November
First egg laid	17 November
Median laying date	25 November
Modal laying date	21 November
95% of nests with eggs	25 November
Last egg laid	3 December
First chick hatched	25 December
One-third of chicks hatched	29 December
Median date of hatching	1 January
Modal date of hatching	29 December
Last chick hatched	8 January
First chick in crèche	19 January
Two-thirds of chicks in crèche	24 January
Median date of entering crèche	24 January
Modal date of entering crèche	24 January
Last chick in crèche	29 January
First date of fledging	8 February
Median date of fledging	25 February
Modal date of fledging	2 March
Last date of fledging	14 March

Diet

Crustaceans dominated the diet of rockhopper penguins at Marion Island during the chick-rearing period in all seasons from 1994/95 to 2001/02 (Table III). Except in 1999/00, they contributed 86–99% of the mass of food collected. In 1999/00, fish formed 79% of the diet in February and 39% for the period January–March.

DISCUSSION

Population estimates 1965/66–1996/97

Van Zinderen Bakker (1971) gives the first estimate of a population of one million rockhopper penguins for both Marion and Prince Edward islands for 1965/66, although it is not known what census method he used to obtain this figure. For northern rockhopper penguins at Amsterdam Island, the average age at first reproduction is 4.7 years and adult survival rate is 84% per year (Guinard *et al.* 1998). For a population in equilibrium, this requires that, for every 100 birds aged 4.7 years or older, there are 85 birds aged between 1.7 and 4.7 years. In such a situation, van Zinderen Bakker's estimate for 1965/66 is equivalent to about 270 000 breeding pairs. In the 1970s, there were thought to be

Table III: The contribution by mass (%) of cephalopods, fish and crustaceans to the diet of rockhopper penguins at Marion Island during the chick-rearing periods of the 1983/84-1984/85 (Brown and Klages 1987) and 1994/95-2001/02 breeding seasons. Mass was not corrected to account for the original biomass of cephalopods and fish ingested. The number of diet samples collected (*n*) is indicated

Cassar	п	Contribution by mass (%)		
Season		Cephalopods	Fish	Crustaceans
1983/84	35	0	0	100
1984/85	31	3 0	5	91
1995/96	30	0	1	99
1996/97 1997/98	30 45	5 0	2 5	93 95
1998/99 1999/00	33 45	1	5 39	94 60
2000/01	44	6	6	88
2001/02	41	1	10	89

35 000 pairs of rockhopper penguins at Prince Edward Island (Cooper and Brown 1990). Subtracting this value from van Zinderen Bakker's estimate leaves a population of 235 000 pairs at Marion Island in 1965/66. Because of the inherent uncertainties with this calculation, and the estimate it is based on, the figure obtained should be treated with caution.

In the 1973/74 breeding season, the population of rockhopper penguins at Marion Island was estimated from ground counts to be 424 600 birds (here taken to represent 212 300 pairs; Watkins 1987), but in the period 1974-1977 only 93 286 pairs were counted (Williams et al. 1975, 1979, Siegfried et al. 1978). The 1973/74 count was conducted along c. 75% of the island's coastline (not including Crawford and Triegaardt bays) during the months of January-March 1974 (Williams et al. 1975), so would not have accounted for breeders that failed beforehand. The 1974-1977 count was conducted in January and February (actual year(s) of counts not given) and was thought to have included 75% of the total breeding population (Siegfried et al. 1978), so again may be regarded as an underestimate. Data given in Siegfried et al. (1978) can be interpreted to show that Crawford and Triegaardt bays were surveyed during the period 1974-1977. The large difference (more than a factor of two) between these two 1970s counts that overlapped in time is puzzling.

For 1987/88, a count of the entire island between 26 November and 9 December gave a total of 137 652 breeding pairs (Cooper and Brown 1990, JC unpublished data). Counts were recorded for similar sections to those used during the period 1994/95–2002/03

(Table I). These early estimates vary widely, reflecting the difficulty in conducting accurate counts and the different times of the surveys. The four estimates between 1965/66 and 1987/88 have a mean of about 169 000 pairs (*SD* 66 000 pairs), a value not dissimilar to the estimates of 173 000 pairs for 1994/95 and 150 000 pairs for 1996/97 (Table I). The mean for the six estimates up until 1996/97 is 167 000 pairs (*SD* 52 000 pairs).

Population trend

From 1983/84 to 2002/03, there was a significant decrease in the number of rockhopper penguins breeding at three small colonies (Trypot Hole, Trypot Fault, Van den Boogard River) in north-eastern Marion Island (Cooper et al. 1997, Woehler et al. 2001, Fig. 2). From 1994/95 to 2002/03, there was a significant decrease in the number of rockhopper penguins in sections in the north-east and south-west of Marion Island that account for one-quarter to one-third of the overall population. From 1994/95 to 2001/02, there was a persistent decrease in the three estimates of the overall population at Marion Island. Assuming an error of 20% on counts, the largest thought to apply for any sector counted in 1996/97, the minimum population in 1994/95 would have been 138 000 pairs and the maximum population in 2001, 80 000 pairs. This indicates a substantial decrease of at least 42% over the period 1994/95-2001/02. Estimates of the decrease in number of breeding rockhopper penguins at Marion Island between 1994/95 and 2002/03, based on counts at the three small monitored colonies, of two sections of the island and of the total population range from 20-61%.

The decrease in the number of rockhopper penguins at Marion Island accords with decreases observed at several other localities in the south-western Atlantic Ocean, south-western Indian Ocean and off New Zealand (Moors 1986, Cunningham and Moors 1994, Ellis *et al.* 1998, Guinard *et al.* 1998, Woehler *et al.* 2001).

In December 2001, 31 655 pairs of rockhopper penguins were counted at Prince Edward Island. Most birds were on eggs and a few small chicks were present. Assuming that 70% of nests hatched chicks (Cooper *et al.* 1997), the total breeding population for 2001/02 was considered to be about 45 000 pairs (Ryan *et al.* 2003). The population in the 1980s was thought to be about 35 000 pairs (Cooper and Brown 1990). The higher estimate for 2001/02 may have resulted from greater coverage in that year and from bias introduced from counting loafing birds as breeders in colonies that were observed at a distance. Therefore, the population at Prince Edward Island appears to have been stable since the 1980s (Ryan *et al.* 2003). This contrasts with the decrease recorded at Marion Island over the same time period.

Dissimilarity in trends of rockhopper penguins has been observed in other regions. The population of the northern subspecies decreased at Amsterdam Island between 1972 and 1994, whereas at St Paul Island, 80 km distant, it increased over the same period (Guinard *et al.* 1998). There were large decreases of southern rockhopper penguins at the Falkland Islands, but the number breeding in Chile and Argentina apparently remained stable during the 1980s and 1990s (Bingham 1998b).

Trends in the numbers of rockhopper penguins breeding at Trypot Hole, Trypot Fault and Van den Boogaard River were significantly related to each other during the seasons 1983/84-1995/96 (Cooper et al. 1997). These significant relationships persisted for the period 1983/84-2002/03. All three colonies are located in north-eastern Marion Island, and the correlation was strongest for the colonies at Trypot Hole and Trypot Fault, which are in close proximity to each other. The significant relationships may be influenced by environmental conditions before or at the onset of breeding (Cooper and Lutjeharms 1992, Cooper et al. 1997). The sometimes dissimilar trends over wider scales, e.g. between the north-east and south-west of Marion Island and between Marion and Prince Edward islands, suggest that any such influence is relatively local in nature and that monitoring over wider areas is required to ascertain trends in the overall population.

Breeding success

Estimates of mean age at first breeding (4.7 years) and adult survival (84% per year) measured at Amsterdam Island (Guinard et al. 1998) require that pairs fledge on average 0.64 chicks for the population to remain in equilibrium. This assumes that fledglings departing to sea have the same survival as adults, that chicks fledge at an age of 0.7 years and that all birds aged 4.7 years or older breed. The incubation period of about 39 days (Williams 1980a) and the fledging period of about 70 days (Marchant and Higgins 1990) together last for about 0.3 years. At Amsterdam Island, survival of first-year birds was estimated to be 39% per year (Guinard et al. 1998). In some years all pairs may not breed (Cooper et al. 1997) and for the adult population there may not be an equal sex ratio. Therefore, for equilibrium, breeding success would need to be >0.64 chicks per pair. However, two rockhopper penguins at Amsterdam Island bred at two years of age (Guinard *et al.* 1998), so there is potential for birds to start breeding when younger than 4.7 years.

At Marion Island during the period 1975-1977, rockhopper penguins fledged on average 0.35 chicks per pair (Williams 1980a). From 1985/86-1995/96, they fledged on average 0.48 chicks per pair (Cooper et al. 1997). From 1994/95-2002/03, the average was 0.40 chicks per pair. These values all are considerably lower than the rate required for a population to remain in equilibrium. The two last values may be underestimates because some chicks leave colonies before the numbers of chicks in crèches are counted. Counts of chicks in crèches were made about 28 February, but chicks may fledge from 8 February. In 1994/95, the median date of fledging was 25 February, whereas most chicks fledged on 2 March (Table II). However, at Trypot Hole in 1994/95, the number of chicks that fledged was overestimated because 15 chicks died after entering the crèche (Marine & Coastal Management unpublished data).

At Campbell Island, where there has been a large decrease in the population (Cunningham and Moors 1994), pairs fledged on average 0.47-0.51 chicks per year (Marchant and Higgins 1990), below the 0.64 required to maintain equilibrium. At Macquarie Island, 0.73 chicks per pair reached the crèche stage (Warham 1963) and at Falkland Islands 77% of pairs fledged chicks (Strange 1982). As observed for Amsterdam Island (Guinard et al. 1998) and Campbell Island (Cunningham and Moors 1994), it appears that the decrease at Marion Island is at least partly attributable to inadequate reproduction. However, age at first breeding and survival have not yet been measured at Marion Island, so the possibility that reduced survival brought about the decrease in the population cannot be excluded.

Breeding success was especially poor in 1998/99 (Fig. 4a), when there also was a large decrease in mass of males and females arriving at breeding colonies (Fig. 4b). It is of interest that this was one year after a large ENSO (*El Niño* Southern Oscillation) event in 1997/98 that affected breeding by several seabirds at Marion Island (Crawford *et al.* 2003).

Timing of breeding

The timing of breeding in 1994/95 (Table II) agreed with the approximate schedule reported by Cooper and Brown (1990). At Macquarie Island, females return to breeding colonies on average 6.5 days after males (Warham 1963). At Marion Island, there also is a tendency for females to return later than males.

Throughout their distribution, rockhopper penguins generally breed between August and March, perhaps starting later at higher latitudes (Marchant and Higgins 1990). However, adults arrive at Marion Island about 10 days later than would be expected from the sea surface temperature there (Marchant and Higgins 1990). At Macquarie Island laying occurs from 8 to 18 November and at Campbell Island from 6 to 15 November (Warham 1963, Marchant and Higgins 1990). Although both these localities are at higher latitudes, laying is earlier than at Marion Island (17 November -3 December).

Mass of adults on arrival at colonies and of chicks at fledging

The generally persistent decrease in the mass of rockhopper penguins arriving at Marion Island during the seasons 1994/95–2002/03 indicates that the availability of food prior to breeding may have decreased. Mass on arrival of males and females was significantly related, suggesting that both sexes were influenced similarly. For both sexes there was a partial recovery in the mass on arrival in 1999/00 (Fig. 4b), when the contribution of fish to the diet during the chick-rearing period was markedly higher than in other seasons (Table III).

Rockhopper penguins lose mass while breeding (Marchant and Higgins 1990), so that a lower mass on arrival at breeding colonies may increase the likelihood of nest failure. From 1994/95 to 2002/03, reproductive success was positively related to mean mass on arrival of males and females.

At Marion Island, the proportion of rockhopper penguins that breeds varies between seasons (Cooper *et al.* 1997). A reduced proportion of birds breeding may have contributed to the decrease in the breeding population and to the significant relationship observed between mass on arrival and numbers breeding at the three monitored colonies.

Unlike the decrease of mass of adults on arrival at colonies from 1994/95 to 2002/03, the mass of chicks at fledging tended to be higher in the most recent seasons (Fig. 4c). This suggests that adults use different feeding areas before breeding and while feeding chicks. Their distribution during the non-breeding period is not well known. A few sightings at sea indicate possible movement along the Subtropical Convergence (Marchant and Higgins 1990). Rockhopper penguins from Falkland Islands appear to move north after moulting and are at sea for six months (Strange 1982). Greater insight into the distribution of adults from Marion Island when not breeding would be valuable in understanding factors that influence their mass on arrival at breeding colonies.

Although mass of chicks at fledging was often

higher after 1997/98 than in earlier seasons, breeding success was lower from 1998/99 to 2002/03 than from 1994/95 to 1997/98 (Fig. 4a, b). When food is scarce, chicks of low mass are more likely to die than when food is abundant, leading to a disproportionate number of heavy chicks surviving (Williams and Croxall 1990).

In each of the nine seasons for which it was measured, the mass of chicks at fledging was lower than that reported for the Falkland Islands (2.22 kg, Strange 1982). In all seasons except 1997/98, when mean mass at fledging was 2.13 kg, it was lower than that reported for Campbell Island (1.99 kg, Cunningham and Moors 1994). Measurements of birds at Campbell and Falkland islands (Marchant and Higgins 1990) do not suggest that they are noticeably larger than those at Marion Island. As suggested by Cunningham and Moors (1994) for Campbell Island, the low mass at fledging may decrease survival of first-year birds.

Diet

At Marion Island during 1973 and 1974, the diet of rockhopper penguins included euphausiids (Williams and Laycock 1981). During the seasons 1983/84-1985/86, crustaceans (85% by mass), mainly Nauticaris marionis and Euphausia vallentini, constituted most of the food, with fish (10%) and cephalopods (5%) of lesser importance (Brown and Klages 1987). The proportion of crustaceans in the diet was high during early chick rearing. Then, proportions of fish and cephalopods increased to peak in about late February, before decreasing sharply. The diet of chicks in their last two weeks before fledging was almost exclusively crustaceans. These changes were thought to be related to foraging strategy, with crustaceans being taken inshore during the guard-stage and pelagic fish and cephalopods offshore when adults are freed to travel farther (Brown and Klages 1987, Adams and Brown 1989). Feeding was believed to be inshore again in the final two weeks of chick rearing, after breeding by macaroni penguins Eudyptes chrysolophus, which also feed mainly on crustaceans at Marion Island, had ended (Brown and Klages 1987). In every season from 1994/95 to 2001/02, crustaceans again dominated the diet. This proportion would have been lower had it been corrected to account for the original biomass of fish ingested (Brown and Klages 1987).

If inadequate supplies of food are responsible for the poor breeding success of rockhopper penguins at Marion Island, and hence the population decrease, availability of crustaceans is likely to be lower than previously. This could result from an altered distribution of prey, as postulated for Campbell Island (Cunningham and Moors 1994) and Amsterdam Island (Guinard *et al.* 1998), decreased abundance of prey, or competition with other predators for food. Pomfret *Brama brama*, a teleost of the family Bramidae found in the North Atlantic Ocean, off south-western Africa, Australia, New Zealand and Chile (Smith and Heemstra 1986), has recently been caught near Marion Island by longline boats targeting Patagonian toothfish *Dissostichus eleginoides*, suggesting increased sea temperatures there (B. P. Watkins, Marine & Coastal Management, *in litt.*), which have been demonstrated by Mélice *et al.* (in press).

At Prince Edward Island, where numbers of rockhopper penguins are thought to be stable, the population of macaroni penguins has probably decreased (Ryan *et al.* 2003). At Marion Island during January and February, rockhopper penguins are thought to forage 4–157 km from breeding colonies (early chick rearing) and macaroni penguins 59–303 km (late chick rearing, Brown 1987). Dietary segregation of these two penguin species is considered incomplete (Brown and Klages 1987, Adams and Brown 1989). Further information on the extent of overlap of feeding grounds of these and other predators of euphausiids is required in order to evaluate the extent of possible competition for resources.

Regardless of the reasons for scarcity of food, several factors combine to indicate that an inadequate supply of food has been responsible for the decrease in the number of rockhopper penguins at Marion Island. These include poor breeding success, decreasing masses of males and females on arrival at the start of the breeding season and a low mass of chicks at fledging.

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Eastern rockhopper penguins at Marion Island (photo B. M. Dyer)