

## BREEDING NUMBERS AND SUCCESS OF *EUDYPTES* PENGUINS AT MARION ISLAND, AND THE INFLUENCE OF MASS AND TIME OF ARRIVAL OF ADULTS

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### Abstract

At sub-Antarctic Marion Island, there was substantial correlation in the numbers of adults breeding at study colonies of macaroni penguins (*Eudyptes chrysolophus*) over 26 years, as there was also for eastern rockhopper (*E. chrysocome filholi*) over 22 years, suggesting that overwintering conditions may influence the proportions of birds breeding. For both species the time of arrival of females for breeding, and for rockhopper penguins the mass of females on arrival, was significantly related to breeding success. Therefore, overwintering conditions may also affect breeding success. Trends in breeding success between study colonies were more strongly correlated for macaroni penguins than for rockhopper penguins. Macaroni penguins have a greater foraging range than rockhopper penguins when breeding, and may be more influenced at this stage by wider-scale environmental phenomena. For macaroni penguins, breeding success was significantly correlated with mass of chicks at fledging. For both species, mass on arrival of males was significantly correlated with that of females. Although both species had low masses on arrival after the El Niño Southern Oscillation event of 1997/98, there was no significant correlation in mass on arrival between the two species. It is likely that at Marion Island their overwintering grounds are different.

### Résumé

A l'île Marion, île subantarctique, on observe une corrélation importante sur 26 années dans le nombre d'adultes de gorfous macaroni (*Eudyptes chrysolophus*) se reproduisant dans les diverses colonies étudiées, ce qui est aussi le cas chez le gorfou sauteur (*E. chrysocome filholi*) sur une période d'observation de 22 années. Ceci laisse entendre que les conditions hivernales peuvent influencer sur la proportion des oiseaux reproducteurs. Chez ces deux espèces, la date d'arrivée des femelles au site de reproduction et, pour le gorfou sauteur, le poids des femelles à l'arrivée au site, sont étroitement liés au succès reproductif. De ce fait, les conditions hivernales peuvent également affecter ce succès. Les tendances du succès reproductif entre les diverses colonies à l'étude affichent une corrélation plus marquée chez les gorfous macaroni que chez les gorfous sauteurs. Les premiers ont un secteur d'alimentation plus étendu lors de la reproduction et pourraient, à ce stade, être plus influencés par les phénomènes environnementaux à grande échelle. Chez le gorfou macaroni, le succès reproductif est plus étroitement lié au poids des jeunes à la première mue. Chez les deux espèces, le poids des mâles à l'arrivée présente une nette corrélation avec celui des femelles. Bien que les deux espèces aient eu un poids peu élevé à l'arrivée après l'événement d'Oscillation australe El Niño de 1997/98, on n'observe pas de corrélation importante du poids à l'arrivée entre les deux espèces. Il est probable que les lieux d'hivernation à l'île Marion soient différents.

### Резюме

На субантарктическом о-ве Марион наблюдалась значительная корреляция численности размножающихся в исследуемых колониях взрослых особей золотоволосых пингвинов (*Eudyptes chrysolophus*) на протяжении 26 лет, а также восточных хохлатых пингвинов (*E. chrysocome filholi*) на протяжении 22 лет, что свидетельствует о возможном влиянии условий перезимовки на долю размножающихся птиц. Время прибытия самок на участок размножения для обоих

видов и масса самок по прибытии для хохлатых пингвинов были существенно связаны с репродуктивным успехом. Следовательно, условия перезимовки могут также влиять на репродуктивный успех. Тенденции изменения репродуктивного успеха между изучаемыми колониями были более сильно скоррелированы для золотоволосые пингвинов, чем для хохлатых пингвинов. При размножении золотоволосые пингвины имеют больший ареал кормодобывания, чем хохлатые пингвины, и могут больше подвергаться влиянию широкомасштабных явлений окружающей среды на этой стадии. Для золотоволосых пингвинов репродуктивный успех сильно зависел от массы птенцов при оперении. Для обоих видов существовала значительная корреляция между массой самцов и самок по прибытии. Хотя оба вида имели низкую массу по прибытии после события Эль-Ниньо/Южное колебание 1997/98 г., значительной корреляции массы по прибытии между этими двумя видами не было. Скорее всего, у них различные участки зимовки на о-ве Марион.

### Resumen

En la isla subantártica Marion se ha observado por 26 años una correlación significativa en el número de pingüinos macaroni (*Eudyptes chrysolophus*) adultos que se reproducen en las distintas colonias estudiadas, y una correlación similar, por 22 años, para el pingüino de penacho amarillo (*E. chrysocome filholi*), que indicarían que las condiciones durante el invierno pueden afectar la proporción de aves que se reproducen. Para ambas especies, la correlación entre el éxito de la reproducción y la fecha de arribo de las hembras a la colonia de reproducción, y en el caso del pingüino de penacho amarillo, el peso de las hembras al arribo, fue significativa. Por lo tanto, las condiciones durante el invierno también pueden afectar el éxito de la reproducción. Las correlaciones entre las tendencias del éxito de la reproducción de las colonias estudiadas fueron más marcadas para los pingüinos macaroni que para los pingüinos de penacho amarillo. Durante la época de la reproducción, el pingüino macaroni cubre un área más extensa en los viajes de alimentación que el pingüino de penacho amarillo, y por lo tanto podría ser afectado en mayor medida por los fenómenos ambientales que se dan en una escala más extensa. En el caso de los pingüinos macaroni, el éxito de la reproducción se correlacionó significativamente con el peso de los polluelos al emplumecer. La correlación entre el peso al arribo de los machos y de las hembras fue significativa para ambas especies. Si bien el peso de arribo de las dos especies fue menor después del fenómeno El Niño y la Oscilación Austral de 1997/98, no hubo una correlación significativa entre el peso al arribo de ambas especies. Es probable que los lugares donde ambas especies pasan el invierno en Isla Marion sean distintos.

Keywords: arrival, breeding proportion, breeding success, *Eudyptes*, macaroni penguin, mass, rockhopper penguin, CCAMLR

### Introduction

Two species of *Eudyptes* (crested) penguins breed at Marion Island (46.9°S 37.9°E), one of two islands in the sub-Antarctic Prince Edward Islands group, a South African territory in the southwest Indian Ocean. They are the macaroni penguin (*E. chrysolophus*) and the eastern rockhopper penguin (*E. chrysocome filholi*). For both species, the numbers of birds estimated to breed at Marion Island decreased markedly after 1994/95: macaroni penguins from 430 000 to 356 000 pairs; and rockhopper penguins from 173 000 to 67 000 pairs. The decreases are thought to result from insufficient food, possibly attributable to climate change, resulting, *inter alia*, in reduced breeding success (Crawford et al., 2003a, 2003b). Both land and sea-surface temperatures (SST) at Marion Island increased prior to the decreases and there was a marked increase in SST anomalies at Marion Island after 1995 (Smith, 2002; Mélice et al., 2003). There

were decreases at Marion Island in populations of other seabirds whose foraging ranges while breeding are limited, notably gentoo penguins (*Pygoscelis papua*) and Crozet shags (*Phalacrocorax [atriceps] melanogenis*) (Crawford et al., 2003c, 2003d, 2003f). The major El Niño Southern Oscillation (ENSO) event of 1997/98 influenced the breeding of many seabirds at Marion Island (Crawford et al., 2003e).

At several other sub-Antarctic localities, ranging from the southwest Atlantic to islands south of New Zealand, decreases of macaroni and rockhopper penguins (the same and other subspecies) have been reported (Moors, 1986; Croxall et al., 1988; Cooper, 1992; Cunningham and Moors, 1994; Isaksen et al., 1997; Woehler and Croxall, 1997; Bingham, 1998; Ellis et al., 1998; Guinard et al., 1998; Trathan et al., 1998; BirdLife International, 2000; Woehler et al., 2001; Bingham, 2002; Clausen and Huin, 2003; Puetz et al., 2003). For some of these decreases, an altered availability of food brought

about through climate change was suggested as a possible, even probable, cause (e.g. Moors, 1986; Cunningham and Moors, 1994).

After breeding, crested penguins depart to sea to fatten up before returning to their breeding localities to moult. During moulting, they are ashore for several weeks, the period varying between species and breeding localities, and do not feed. Thereafter, they leave again to sea to regain condition before breeding. Usually males arrive at colonies several days earlier than females (Marchant and Higgins, 1990). Macaroni penguins leave Marion Island after moulting by 25 April, before returning in late October and early November at the start of the next breeding season (Rand, 1954; Crawford et al., 2003a); hence they are absent from the island for six months. Rockhopper penguins also are absent from breeding localities for about six months (Williams, 1995). After returning to their breeding colonies, crested penguins fast for periods that differ between species and sexes and average 33–43 days (Croxall and Davis, 1999). At this time courtship occurs and eggs are laid. Soon afterwards males leave to feed and then return to relieve their partners, the incubation shifts of the two parents lasting 10–14 days on average (Marchant and Higgins, 1990). During fasts, macaroni penguins rely mainly on lipid reserves (Williams et al., 1992).

At Marion Island, the numbers breeding and the breeding success of macaroni penguins have been monitored annually at three localities since 1979/80. For rockhopper penguins, numbers breeding have been monitored at three localities since 1983/84 and breeding success since 1985/86 (Cooper et al., 1987). Since 1994/95, the breeding success of macaroni penguins has been recorded at a fourth locality. Also since 1994/95, for both species the mass of adults on arrival at colonies to breed and of fledglings ready to depart to sea has been measured, following CCAMLR Ecosystem Monitoring Program (CEMP) protocols (Crawford et al., 2003a, 2003b). Over the period for which the mass of adults was recorded, the approximate dates of arrival of adults to breed may be gauged. This paper reports trends in the numbers breeding and breeding success at study colonies of the two *Eudyptes* penguins at Marion Island from 1978/79 to 2004/05, and considers factors that may be influencing these parameters.

## Methods

### Macaroni penguin

For macaroni penguins, counts of the numbers of incubating adults (taken to represent breeding

pairs) were made at Van den Boogaard River, Macaroni Bay north and Archway Bay, at the northeast of Marion Island (Figure 1), in each season from 1979/80 to 2004/05, as close as possible to 20–24 November, when most birds are incubating (Cooper and Brown, 1990; Cooper et al., 1997). These colonies were selected because they are discrete and of relatively small size, enabling accurate counts to be undertaken from their boundaries without causing excessive disturbance (Cooper et al., 1997). Dates of counts for 1994/95–2004/05 are shown in Table 1. At the same colonies, counts of the numbers of chicks in crèches were made as close as possible to 10 February (Cooper et al., 1997). From 1994/95 to 2004/05, each count was made three times on the same day by the same observer and the mean was calculated. For each season, breeding success was calculated as the number of chicks fledged per pair.

From 1994/95 to 2004/05, similar counts were undertaken of portions of the Bullard Beach colony, south of the other three colonies (Figure 1), to estimate breeding success. The portions investigated, which differed from year to year, were relatively discrete and clearly mapped. The colony at Bullard Beach is larger than those at the other three localities (Crawford et al., 2003a).

The arrival mass of adults at breeding colonies was measured at Bullard Beach for each season from 1994/95 to 2004/05. The sex of adults was identified using bill measurements. Males are larger than females, have longer bills and arrive at colonies earlier than females (Marchant and Higgins, 1990). For the same period, but at different colonies, the mass at fledging of chicks that had left the colonies, or were about to leave, was obtained. Dates when measurements were undertaken and sample sizes are indicated in Table 2. Mass was measured by catching a bird and placing it in a harness, which was then suspended from a spring balance that weighed to an accuracy of 10 g. After weighing, both adults and chicks were marked with a harmless food colorant so that they would not be weighed a second time.

Means of body masses of adults and chicks, as well as breeding success, were calculated  $\pm 1$  standard deviation (SD). All years for which data were available were given equal weighting.

The dates of weighing of males and females were used as surrogates of the timing of their arrival at the island. A lookout was kept for returning birds from about the beginning of October in each season. Birds were weighed when about 200 of that sex had arrived. As landing beaches were not checked

Table 1: Dates on which counts were undertaken of numbers of pairs of macaroni and rockhopper penguins breeding in the long-term study colonies, 1994/95–2004/05.

Season	Macaroni penguin			Rockhopper penguin		
	Van den Boogaard River	Macaroni Bay	Archway Bay	Van den Boogaard River	Trypot Hole	Trypot Fault
1994/95	4 Dec	20 Nov	21 Nov	4 Dec	4 Dec	4 Dec
1995/96	14 Nov	14 Nov	14 Nov	4 Dec	4 Dec	4 Dec
1996/97	15 Nov	15 Nov	15 Nov	6 Dec	6 Dec	6 Dec
1997/98	21 Nov	20 Nov	20 Nov	9 Dec	9 Dec	9 Dec
1998/99	24 Nov	24 Nov	24 Nov	12 Dec	9 Dec	9 Dec
1999/00	20 Nov	20 Nov	19 Nov	9 Dec	9 Dec	9 Dec
2000/01	18 Nov	18 Nov	18 Nov	11 Dec	11 Dec	11 Dec
2001/02	7 Dec	16 Nov	16 Nov	7 Dec	7 Dec	7 Dec
2002/03	19 Nov	19 Nov	19 Nov	9 Dec	9 Dec	9 Dec
2003/04	20 Nov	19 Nov	19 Nov	10 Dec	10 Dec	10 Dec
2004/05	20 Nov	20 Nov	20 Nov	9 Dec	9 Dec	9 Dec

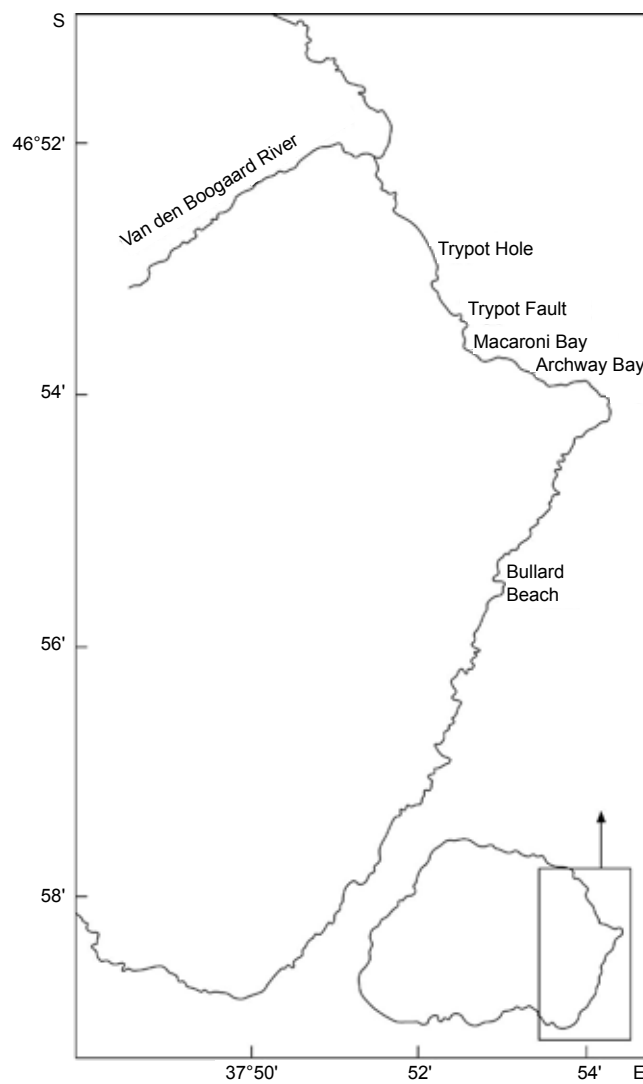


Figure 1: The locations of study colonies of macaroni and rockhopper penguins at Marion Island.

Table 2: Dates on which mass of males and females returning to breed and of chicks fledging were obtained for macaroni and rockhopper penguins, 1994/95–2004/05. Sample sizes are indicated.

Season	Macaroni penguin					
	Male		Female		Fledgling	
	Date	<i>n</i>	Date	<i>n</i>	Date	<i>n</i>
1994/95	15 Oct	114	22 Oct	100	18–25 Feb	129
1995/96	9 Oct	128	22 Oct	17	19–20 Feb	175
1996/97	14 Oct	100	23 Oct	100	11 Feb	225
1997/98	9 Oct	100	16 Oct	100	8 Feb	249
1998/99	12 Oct	145	16 Oct	44	20 Feb	198
1999/00	12 Oct	100	14 Oct	100	17–22 Feb	250
2000/01	12 Oct	100	15 Oct	100	17–24 Feb	250
2001/02	2 Oct	100	10 Oct	100	7 Feb	250
2002/03	2 Oct	100	11 Oct	100	7–8 Feb	250
2003/04	7 Oct	100	13 Oct	100	6–8 Feb	250
2004/05	4 Oct	100	11 Oct	100	28 Jan	250

Season	Rockhopper penguin					
	Male		Female		Fledgling	
	Date	<i>n</i>	Date	<i>n</i>	Date	<i>n</i>
1994/95	3 Nov	113	7 Nov	84	9–15 Mar	106
1995/96	3 Nov	37	7 Nov	40	5–13 Mar	135
1996/97	6 Nov	100	10 Nov	100	3 Mar	250
1997/98	10 Nov	100	11 Nov	100	6 Mar	250
1998/99	12 Nov	100	14 Nov	100	12–17 Mar	186
1999/00	2 Nov	100	8 Nov	100	1–3 Mar	250
2000/01	3 Nov	100	7 Nov	100	2–5 Mar	250
2001/02	3 Nov	100	7 Nov	102	28 Feb–3 Mar	250
2002/03	8 Nov	100	14 Nov	80	3 Mar	250
2003/04	6 Nov	100	10 Nov	100	2–4 Mar	250
2004/05	28 Oct	100	3 Nov	100	19 Feb	250

daily, dates of weighing will be an approximate indication of the first day of arrival of substantial numbers of birds.

#### Rockhopper penguin

Counts of the numbers of occupied nests (taken to represent breeding pairs) of rockhopper penguins at Van den Boogaard River, Trypot Hole and Trypot Fault at the northeast of Marion Island (Figure 1) were made annually from 1983/84 to 2004/05, as close as possible to 4 December when all eggs had been laid (Crawford et al., 2003b). These colonies were selected because they are discrete and of relatively small size, enabling accurate counts to be undertaken from their boundaries without causing excessive disturbance (Cooper et al., 1997). Dates of counts for 1994/95–2004/05 are shown in Table 1. At the same colonies, counts of the numbers of chicks in crèches were made as close as possible to 28 February, about the time that the last

chicks enter crèches (Crawford et al., 2003b). From 1994/95 to 2004/05, each count was made three times on the same day by the same observer and the mean was calculated. For each season, breeding success was calculated as the number of chicks fledged per pair.

For each of the 1994/95–2004/05 breeding seasons, the arrival mass at breeding colonies of males and females and the mass of chicks at fledging were obtained. Sexes of adults 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  $45.7 \pm 1.4$  mm and for females  $40.6 \pm 1.7$  mm (Williams, 1980). Dates when measurements were undertaken and sample sizes are indicated in Table 2.

Dates of weighing and arrival were selected in a similar fashion to those of macaroni penguins, except that a lookout was kept for returning

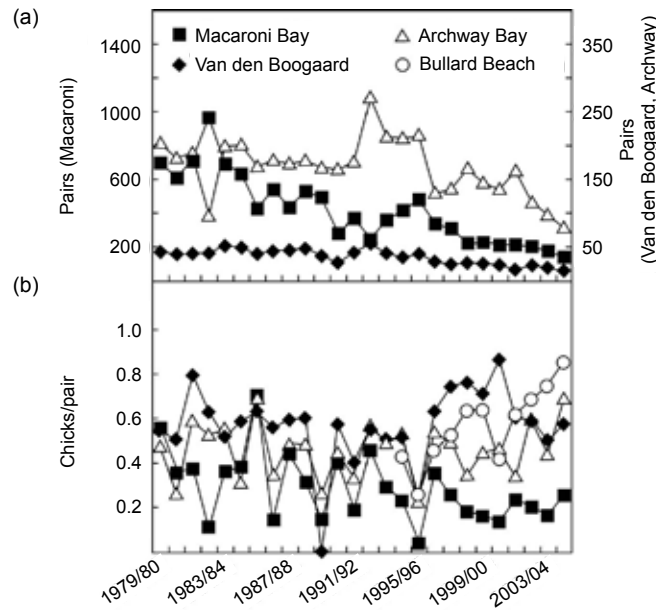


Figure 2: Trends for macaroni penguins at Marion Island in: (a) numbers of pairs breeding at Van den Boogaard River, Macaroni Bay and Archway Bay, and (b) breeding success at these three localities and Bullard Beach, 1979/80–2004/05.

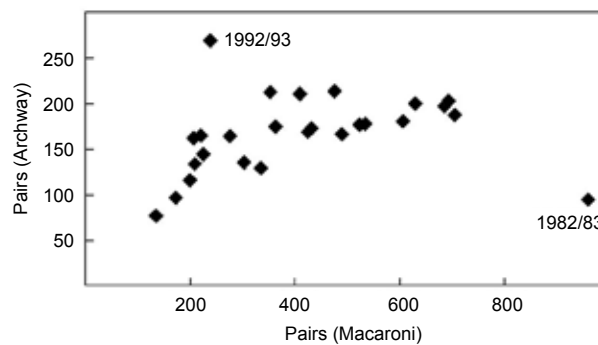


Figure 3: The relationship between numbers of pairs of macaroni penguins breeding at Macaroni Bay and Archway Bay, 1979/80–2004/05. The seasons for the outlying points are indicated.

rockhopper penguins from about the end of October. Methods used to obtain weights were the same as described for macaroni penguins.

## Results

### Macaroni penguin

The numbers of macaroni penguins breeding at each of the three long-term study colonies decreased between 1979/80 and 2004/05 (Figure 2). Numbers breeding at Van den Boogaard River were significantly related to numbers breeding at both Macaroni Bay ( $r = 0.671, n = 26, P < 0.001$ ) and

Archway Bay ( $r = 0.721, n = 26, P < 0.001$ ). There was no significant relationship between the numbers breeding at Macaroni Bay and Archway Bay ( $r = 0.235, n = 26$ ). In 1982/83, there were large increases and decreases in numbers breeding at Macaroni Bay and Archway Bay respectively, and penguins may have moved between the two colonies (Cooper et al., 1997). When this breeding season is omitted, the relationship becomes significant ( $r = 0.524, n = 25, P < 0.01$ ) (Figure 3).

There was no long-term trend in breeding success at any of the three long-term study colonies (Figure 2). Generally, breeding success was higher

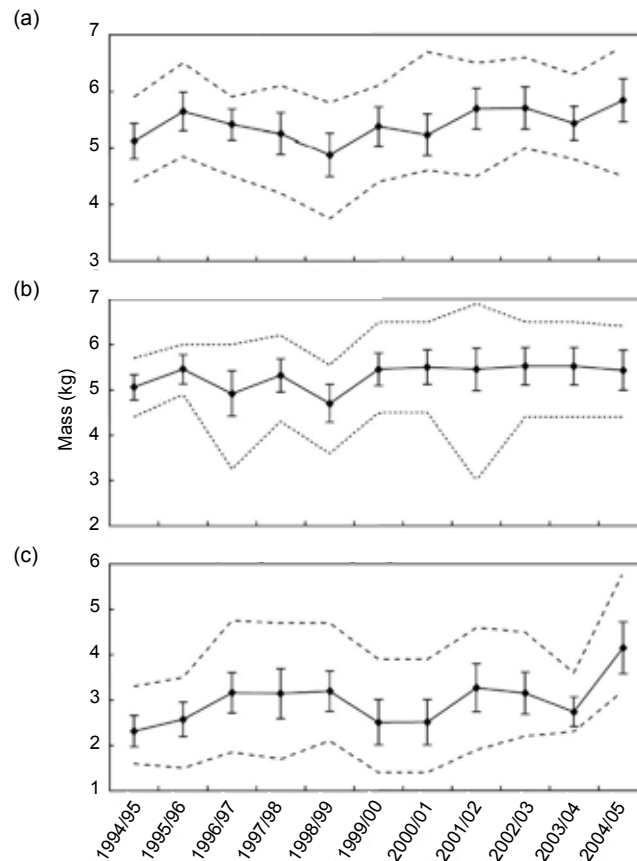


Figure 4: Trends for macaroni penguins at Marion Island in mass on arrival of: (a) males, (b) females and (c) in mass at fledging of chicks, 1994/95–2004/05. For each season, means are shown with standard deviations and ranges.

at Van den Boogaard River than at the other two colonies and lowest at Macaroni Bay. Breeding success at Archway Bay was usually intermediate between levels recorded at the other two colonies. Over the 26-year period, breeding success averaged  $0.57 \pm 0.17$  chicks/pair at Van den Boogaard River,  $0.46 \pm 0.13$  at Archway Bay and  $0.28 \pm 0.15$  at Macaroni Bay. Overall breeding success at the three colonies ranged from 0.10 (1995/96) to 0.69 (1984/85) chicks/pair with an average of  $0.35 \pm 0.13$  chicks/pair.

At the Bullard Beach colonies, breeding success increased between 1994/95 and 2004/05 (Figure 2). Over this period it averaged  $0.56 \pm 0.18$  chicks/pair. In these seasons, the overall breeding success at the four study colonies was between 0.13 and 0.77 chicks/pair (mean  $0.51 \pm 0.18$ ).

Breeding success at Archway Bay was significantly related to that at Van den Boogaard River ( $r = 0.457$ ,  $n = 26$ ,  $P < 0.02$ ) and Macaroni Bay ( $r = 0.460$ ,  $n = 26$ ,  $P < 0.02$ ). Breeding success at Van den Boogaard River was positively, but not significantly, related to that at Macaroni Bay ( $r = 0.194$ ,  $n = 26$ ). Over 11 seasons, breeding success at the

Bullard Beach colonies was positively, but not significantly, related to that at each of the three long-term colonies, the strongest relationship being with the colony at Archway Bay ( $r = 0.573$ ).

The average mass on arrival at Marion Island of male macaroni penguins varied between 4.88 and 5.84 kg (Figure 4). The overall mean was  $5.42 \pm 0.29$  kg. The average mass on arrival of females was between 4.70 and 5.52 kg (Figure 4). The overall mean was  $5.30 \pm 0.28$  kg. The average mass at fledging of macaroni penguin chicks varied between 2.31 and 4.15 kg (Figure 4). The overall mean was  $2.97 \pm 0.52$  kg. The lowest and highest masses recorded for returning males, returning females and fledged chicks were 3.75 and 6.29 kg, 3.00 and 6.25 kg, and 1.40 and 4.30 kg respectively.

Mass of males on arrival was significantly related to that of females ( $r = 0.679$ ,  $n = 11$ ,  $P < 0.05$ ). There was no significant relationship between mass of returning males or females and breeding success.

Dates at which birds returning to Marion Island were caught for weighing varied from 2 October in 2002/03 to 15 October in 1994/95 for males, and

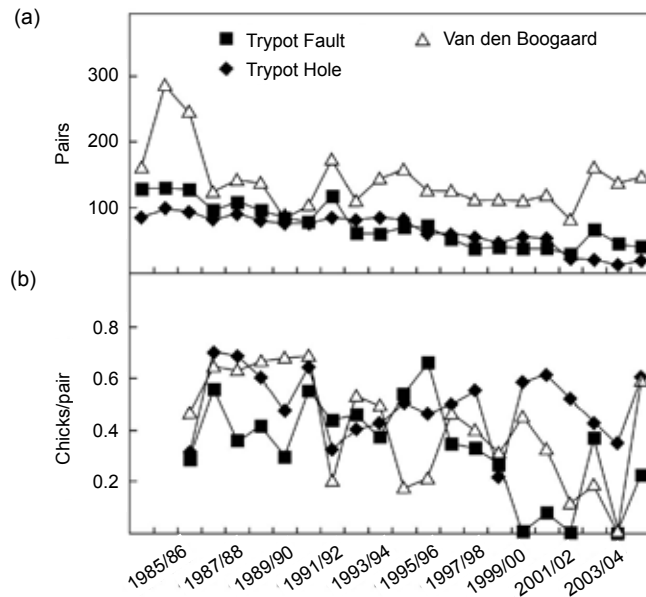


Figure 5: Trends for rockhopper penguins at Marion Island in (a) numbers of pairs breeding, and (b) breeding success at Van den Boogaard River, Trypot Hole and Trypot Fault, 1983/84–2004/05.

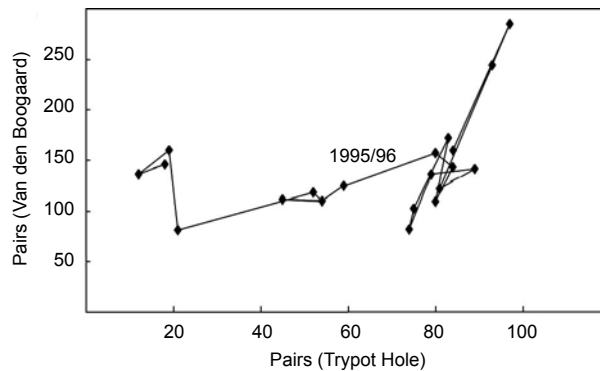


Figure 6: A comparison of the numbers of pairs of rockhopper penguins breeding at Van den Boogaard River and Trypot Hole. From 1995/96 numbers breeding at Trypot Hole were less than 70 pairs and decreased.

10 October in 2001/02 to 23 October in 1996/97 for females (Table 2). Date at weighing of returning birds was negatively related to breeding success for both males ( $r = -0.531$ ,  $n = 11$ , not significant) and females ( $r = -0.762$ ,  $n = 11$ ,  $P < 0.01$ ).

The mass of chicks at fledging was significantly related to overall breeding success ( $r = 0.649$ ,  $n = 11$ ,  $P < 0.05$ ).

### Rockhopper penguin

The numbers of rockhopper penguins breeding at each of the three study colonies decreased between 1983/84 and 2004/05, but only marginally so at Van den Boogaard River (Figure 5). Numbers

breeding at Trypot Fault were significantly related to numbers breeding at both Van den Boogaard River ( $r = 0.663$ ,  $n = 22$ ,  $P < 0.001$ ) and Trypot Hole ( $r = 0.754$ ,  $n = 22$ ,  $P < 0.001$ ). From 1983/84 to 1994/95 there was also a significant relationship between numbers breeding at Van den Boogaard River and Trypot Hole ( $r = 0.907$ ,  $n = 12$ ,  $P < 0.001$ ). After 1994/95, once the colony at Trypot Hole had fallen below 70 pairs, it continued to decrease, whereas the colony at Van den Boogaard River remained stable and even increased in 2002/03 (Figure 6).

There was substantial fluctuation in breeding success at each of the three long-term study colonies (Figure 5). Breeding success was often higher at



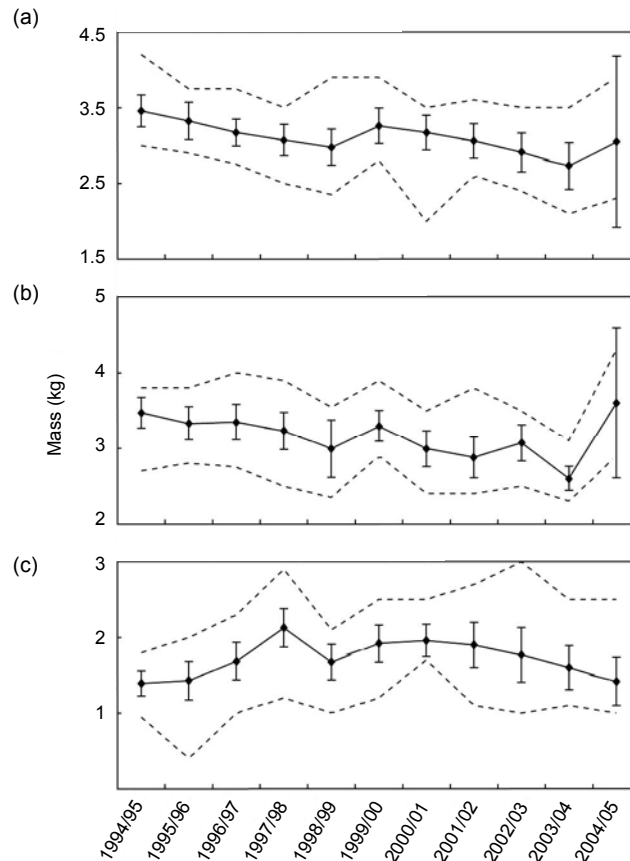


Figure 7: Trends for rockhopper penguins at Marion Island in mass on arrival for breeding of (a) males, (b) females and (c) in mass at fledging of chicks, 1994/95–2004/05. For each season means are shown with standard deviations and ranges.

Trypot Hole than at the other two colonies. Over the 20-year period, it averaged  $0.49 \pm 0.13$  chicks/pair at Trypot Hole,  $0.41 \pm 0.21$  at Van den Boogaard River and  $0.33 \pm 0.19$  at Trypot Fault. Overall breeding success at the three colonies ranged from 0.24 (2003/04) to 0.63 (1990/91) chicks/pair with an average of  $0.44 \pm 0.11$  chicks/pair. Breeding success at Van den Boogaard River was significantly related to that at Trypot Hole ( $r = 0.520$ ,  $n = 19$ ,  $P < 0.02$ ) but relationships between other pairs of colonies were not significant ( $r = 0.095$  and  $0.303$ ).

The average mass on arrival at Marion Island of male rockhopper penguins varied between 2.73 and 3.46 kg (Figure 7). The overall mean was  $3.11 \pm 0.20$  kg. The average mass on arrival of females was between 2.60 and 3.60 kg (Figure 7). The overall mean was  $3.17 \pm 0.29$  kg. The average mass at fledging of rockhopper penguin chicks varied between 1.39 and 2.13 kg (Figure 7). The overall mean was  $1.71 \pm 0.25$  kg. The lowest and highest masses recorded for returning males, returning females and fledged chicks were 2.00 and 4.20 kg, 2.30 and 4.30 kg, and 0.40 and 3.0 kg respectively.

From 1994/95–2003/04, the average mass of male rockhopper penguins returning to Marion Island to breed decreased by 0.73 kg (21%), and that of females by 0.87 kg (25%). In 2004/05, the mass of both sexes increased, that of females markedly (Figure 7). Mass of males on arrival was significantly related to that of females ( $r = 0.696$ ,  $n = 11$ ,  $P < 0.02$ ). Breeding success was positively related to mass of returning males ( $r = 0.552$ ,  $n = 11$ , not significant) and females ( $r = 0.855$ ,  $n = 11$ ,  $P < 0.001$ ).

Dates at which birds returning to Marion Island were caught for weighing varied from 28 October in 2004/05 to 12 November in 1998/99 for males, and 3 November in 2004/05 to 14 November in 1998/99 and 2002/03 for females (Table 2). Date at weighing of returning birds was negatively related to breeding success for both males ( $r = -0.591$ ,  $n = 11$ ,  $P < 0.05$ ) and females ( $r = -0.726$ ,  $n = 11$ ,  $P < 0.05$ ).

The mass of chicks at fledging was not related to breeding success.

### Interspecies comparisons

There were no significant relationships between macaroni penguins and rockhopper penguins for any of the following parameters: overall breeding success, breeding success at Van den Boogaard River (both 1985/86–2004/05), mass of males or females on arrival to breed, dates at weighing of males or females on their return to breed and mass of chicks at fledging (all 1994/95–2004/05). At Van den Boogaard River, the numbers of macaroni and rockhopper penguins breeding in any season were significantly related during the period from 1983/84 to 2004/05 ( $r = 0.364$ ,  $n = 22$ ,  $P < 0.01$ ). The overall numbers of these species breeding at the three monitored colonies were also significantly related ( $r = 0.727$ ,  $n = 22$ ,  $P < 0.001$ ). However, other breeding localities that were not counted every year exist within the same region (Crawford et al., 2003a).

### Discussion

At Marion Island, up until the 1995/96 season, the numbers of macaroni penguins breeding at the three long-term study colonies were significantly related in only one of three comparisons, whereas trends in breeding success were significantly related in all three comparisons, largely as a result of similar trends in chick survival. By contrast, the numbers of rockhopper penguins breeding were significantly related in all three comparisons, but in only one of three comparisons was there a significant relationship in breeding success (Cooper et al., 1997). Based on these results, it was suggested that the proportion of rockhopper penguins breeding may be influenced by environmental conditions before, or at the onset of, breeding, whereas breeding success of macaroni penguins might be influenced by wider-scale phenomena than is the case for rockhopper penguins (Cooper et al., 1997), e.g. the locations of fronts or eddies.

### Numbers breeding

With the longer data series now available, there was substantial correlation between different colonies in the numbers of breeding birds for both species. For rockhopper penguins, in one comparison the trends in numbers breeding diverged once the smaller colony fell below a certain level and continued to decrease, while the other colony remained stable (Figure 6). Because crested penguins rely mainly on lipid reserves during fasts (Williams et al., 1992), birds of low mass returning to colonies may elect not to breed. At Bird Island, South Georgia, following a severe, prolonged winter, 14% of macaroni penguins did not breed and

there was increased adult mortality (Williams and Rodwell, 1992). For blue petrels (*Halobaena caerulea*) at Kerguelen Island, poor body condition early in the breeding season led to a high proportion of birds not breeding and massive desertion of eggs (Chastel et al., 1995). The marked decrease in the mass of adult rockhopper penguins returning to Marion Island between 1994/95 and 2003/04 (Figure 7) may have caused substantial non-breeding in the latter part of this period, contributing to the population decrease (Crawford et al., 2003b).

Information on the at-sea distributions of macaroni and rockhopper penguins from Marion Island outside their breeding seasons is currently lacking. At many other localities, information on the winter distributions of these species is also scarce. Vagrant crested penguins, often immature birds, have been recorded far from their breeding colonies. For example, rockhopper, Fiordland (*E. pachyrhynchus*), Snares (*E. robustus*), erect-crested (*E. sclateri*) and royal (*E. schlegeli*) penguins have all been recorded along the coast of southern Australia (Marchant and Higgins, 1990). Macaroni and rockhopper penguins have been recorded in South Africa (Cooper, 1988).

When not breeding, macaroni penguins are thought to remain in sub-Antarctic waters between about 45° and 65°S (Marchant and Higgins, 1990; Williams, 1995). In winter, southern rockhopper penguins (*E. c. chrysocome*) in the Falkland/Malvinas Islands migrate from their breeding colonies to coastal areas of South America, some 600 km away. Birds from colonies in the north of the Falkland/Malvinas Islands also use areas along the slope of the Patagonian shelf, about 1 400 km northwards. A few birds from the southern breeding colony move about 250 km south of the Falkland/Malvinas Islands (Puetz et al., 2003). Interannual variation is evident, both in the use of different foraging areas and in the time at which the winter migration starts (Puetz et al., 2003).

The large differences at Marion Island in mass on arrival of rockhopper penguins for breeding (Figure 7) suggest that food availability to these birds during winter varies between years. The significant correlations between mass at arrival of males and females for macaroni and rockhopper penguins suggest that both sexes of each species may overwinter in similar areas. Conversely, the lack of any correlation between the two species in mass at arrival suggests that their overwintering grounds are not the same. At Marion Island, there is some overlap in the diets of these two species during breeding (Brown and Klages, 1987; Adams and Brown, 1989). Hence, if they overwintered in the

same region, their condition at the onset of breeding could be expected to be similar. At Macquarie Island, there is some overlap in the diets of royal penguins, once regarded as a subspecies of macaroni penguins (Del Hoyo et al., 1992), and eastern rockhopper penguins (Hull, 1999a). At Kerguelen Island, two closely-related species of prion (*Pachyptila belcheri* and *P. desolata*) have substantial overlap in their diets while breeding, but have distinct winter feeding grounds (Cherel et al., 2002). The ENSO of 1997/98 caused a large decrease in mass at arrival of both macaroni and rockhopper penguins at Marion Island in 1998/99 (Crawford et al., 2003a, 2003b). Probably this ENSO had a wide-scale impact in the southwest Indian Ocean.

### Breeding success

With regard to breeding success, at Marion Island two of three long-term comparisons were significant for macaroni penguins and one of three for rockhopper penguins. Generally, the relationships were stronger for macaroni penguins, suggesting that, while breeding, this species may be more influenced by wider-scale environmental phenomena than rockhopper penguins (Cooper et al., 1997). These findings accord with the foraging ranges of the two species during breeding. At Marion Island in January and February 1985, from deployment of speed meters, it was estimated that rockhopper penguins foraged 4–157 km from breeding colonies (early chick rearing), and macaroni penguins, 59–303 km (late chick rearing; Brown, 1987). One macaroni penguin fitted with a satellite transmitter during brooding foraged 600 km to the south of Marion Island in December 2001 and January 2002 (Akkers, 2002).

At Bird Island, South Georgia, during incubation macaroni penguins travelled long distances on foraging trips: on average 572 km for males and 376 km for females, whereas during chick-rearing trips they averaged 62 km and foraged over the continental shelf (Barlow and Croxall, 2002). At Heard Island, macaroni penguins foraged mainly in the shelf area within a radius of 300 km when breeding (Green et al., 1998). At Macquarie Island, it was estimated that, during breeding, royal penguins travelled further during foraging than rockhopper penguins, providing some segregation in foraging zones (Hull, 1999b). At Staten Island, Tierra del Fuego, southern rockhopper penguins brooding chicks travelled up to 20 km to feed (Schiavini and Rey, 2004). In the Falkland/Malvinas Islands, southern rockhopper penguins foraged both close to colonies (<10 km) and at greater distances (>100 km) when breeding (Boersma et al., 2002).

The mass of adults returning to breed at Marion Island had no influence on the breeding success of macaroni penguins. However, for rockhopper penguins the mass of returning females was significantly related to breeding success. Therefore, feeding conditions of rockhopper penguins during winter may influence breeding success. Whereas over 10 seasons there was a sustained decrease in mass on arrival of rockhopper penguins, mass on arrival of macaroni penguins remained more constant (Figures 4 and 7). At South Georgia, a long-term decrease in mass at arrival for breeding of both sexes of macaroni penguins was associated with a decrease in numbers breeding and reduced reproductive output (Reid and Croxall, 2001).

Over 11 seasons, the approximate date when substantial numbers of adults had returned to breed at Marion Island varied by 13 days for male and female macaroni penguins and by 15 and 11 days for these sexes of rockhopper penguins respectively. The date of return was negatively related to breeding success for both species, significantly so in the case of females, suggesting that a delayed return decreases productivity. At Bird Island, South Georgia, following a severe, prolonged winter, there was a delayed onset of breeding for macaroni penguins (Williams and Rodwell, 1992). In 1987 at the same locality, adults arrived three days later and the mean egg-laying date was three days later compared to three other years (Williams and Croxall, 1991).

At Marion Island, the mass of chicks at fledging was related to breeding success for macaroni penguins but not for rockhopper penguins. When food is scarce, chicks of low mass are more likely to die than when food is abundant. If only heavy chicks survive in such years, the mean mass may be higher than in years when lighter chicks also survive (Williams and Croxall, 1990). This may have caused the lack of a relationship between the two parameters for rockhopper penguins. However, for macaroni penguins, in years of high survival of chicks, fledglings generally had a better condition, as measured by body mass.

### Conclusions

In summary, at Marion Island overwintering conditions probably influence the proportion of adult birds that breed in the following summer for both macaroni and rockhopper penguins. The wintering grounds are not known for either species but are likely to be different, there being poor correlation of arrival dates and masses of the two species. For rockhopper penguins, winter conditions may be an important factor determining the outcome of

breeding. To the extent that they determine the date of arrival at colonies of macaroni penguins, they may influence breeding success of that species as well. For macaroni penguins, environmental conditions during breeding, especially food availability (Crawford et al., 2003a), appear to affect both the outcome of breeding and the condition of chicks at fledging; hence, they are likely to have a substantial impact on future recruitment to the breeding population. For both species, breeding success during 1994/95–2002/03 was thought inadequate to maintain the populations (Crawford et al., 2003a, 2003b). The possibility that reduced survival of adults also contributed to the decrease in the population of rockhopper penguins at Marion Island cannot be discounted (Crawford et al., 2003b).

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#### Liste des tableaux

- Tableau 1: Dates des recensements du nombre de couples reproducteurs de gorfous macaroni et sauteurs dans les colonies ayant fait l'objet d'études à long terme de 1994/95 à 2004/05.
- Tableau 2: Dates d'obtention du poids des mâles et des femelles revenant pour se reproduire et des jeunes à la première mue, tant pour les gorfous macaroni que sauteurs, de 1994/95 à 2004/05. La taille des échantillons est indiquée.

#### Liste des figures

- Figure 1: Emplacement des colonies d'étude des gorfous macaroni et sauteurs de l'île Marion.
- Figure 2: Tendances chez les gorfous macaroni de l'île Marion : (a) nombre de couples se reproduisant à Van den Boogaard River, à la baie Macaroni et à la baie Archway et (b) succès reproductif à ces trois sites et à Bullard Beach de 1979/80 à 2004/05.
- Figure 3: Rapport entre le nombre de couples de gorfous macaroni se reproduisant à la baie Macaroni et à la baie Archway, de 1979/80 à 2004/05. Les saisons correspondant aux points isolés sont indiquées.

- Figure 4: Tendances chez les gorfous macaroni de l'île Marion du poids à l'arrivée : (a) mâles, (b) femelles et (c) poids des jeunes à la première mue, de 1994/95 à 2004/05. Indication, pour chaque saison, des moyennes, des écarts-types et des intervalles.
- Figure 5: Tendances chez les gorfous sauteurs de l'île Marion : (a) nombre de couples se reproduisant et (b) succès reproductif à Van den Boogaard River, Trypot Hole et Trypot Fault, de 1983/84 à 2004/05.
- Figure 6: Comparaison du nombre de couples de gorfous sauteurs se reproduisant à Van den Boogaard River et Trypot Hole. Depuis 1995/96, le nombre de couples se reproduisant à Trypot Hole est inférieur à 70 et en baisse.
- Figure 7: Tendances chez les gorfous macaroni de l'île Marion du poids à l'arrivée : (a) mâles, (b) femelles et (c) poids des jeunes à la première mue, de 1994/95 à 2004/05. Indication, pour chaque saison, des moyennes, des écarts-types et des intervalles.

#### Список таблиц

- Табл. 1: Даты проведения подсчетов числа размножающихся пар золотоволосых и хохлатых пингвинов в колониях, где проводятся многолетние исследования, 1994/95–2004/05 гг.
- Табл. 2: Даты измерения массы возвращающихся на размножение самцов и самок и оперяющихся птенцов золотоволосых и хохлатых пингвинов, 1994/95–2004/05 гг. Показан размер выборки.

#### Список рисунков

- Рис. 1: Местоположение изучаемых колоний золотоволосых и хохлатых пингвинов на о-ве Марион.
- Рис. 2: Тенденции для золотоволосых пингвинов на о-ве Марион: (a) число размножающихся пар, река Ван ден Бугард, бухты Макарони и Арчвей, и (b) репродуктивный успех на этих трех участках и на берегу Буллард, 1979/80–2004/05 гг.
- Рис. 3: Зависимость между числом пар золотоволосых пингвинов, размножающихся в бухтах Макарони и Арчвей, 1979/80–2004/05 гг. Для резко выделяющихся точек показаны сезоны.
- Рис. 4: Тенденции для золотоволосых пингвинов на о-ве Марион: масса по прибытии (a) самцов, (b) самок и (c) масса птенцов при оперении, 1994/95–2004/05 гг. Для каждого сезона показаны средние, их стандартные отклонения и диапазон.
- Рис. 5: Тенденции для хохлатых пингвинов на о-ве Марион: (a) число размножающихся пар и (b) репродуктивный успех, река Ван ден Бугард, залив Трайпот и сброс Трайпот, 1983/84–2004/05 гг.
- Рис. 6: Сравнение числа пар хохлатых пингвинов, размножающихся в районе реки Ван ден Бугард и залива Трайпот. С 1995/96 г. в заливе Трайпот было меньше 70 размножающихся пар и это количество сокращалось.
- Рис. 7: Тенденции для хохлатых пингвинов на о-ве Марион: масса по прибытии к участкам размножения (a) самцов, (b) самок и (c) масса птенцов при оперении, 1994/95–2004/05 гг. Для каждого сезона показаны средние, их стандартные отклонения и диапазон.

#### Lista de las tablas

- Tabla 1: Fechas en las cuales se efectuó un recuento de las parejas de pingüino macaroni y de penacho amarillo que se reproducen en las colonias donde se efectúa un seguimiento a largo plazo, 1994/95–2004/05.
- Tabla 2: Fechas en las cuales se registró el peso de los machos y hembras al arribo a la colonia de reproducción y de los polluelos al emplumecer, tanto para el pingüino macaroni como para el pingüino de penacho amarillo, 1994/95–2004/05. Se indica el tamaño de la muestra.

Lista de las figuras

- Figura 1: Ubicación de las colonias de estudio del pingüino macaroni y del pingüino de penacho amarillo en Isla Marion.
- Figura 2: Tendencias observadas en las colonias del pingüino macaroni en Isla Marion con respecto a: (a) el número de parejas que se reproducen en el Río Van den Boogaard, Bahía Macaroni y Bahía Archway, y (b) el éxito de la reproducción en estas tres localidades y en la Playa Bullard, 1979/80–2004/05.
- Figura 3: Relación entre el número de parejas de pingüinos macaroni que se reproducen en la Bahía Macaroni y la Bahía Archway, 1979/80–2004/05. Se indican las temporadas con desviaciones extremas del promedio.
- Figura 4: Tendencias del peso de los pingüinos macaroni en Isla Marion para: (a) machos al arribo, (b) hembras al arribo, y (c) polluelos al emplumecer, 1994/95–2004/05. Se muestra el promedio, la desviación estándar y el rango para cada temporada.
- Figura 5: Tendencias observadas en las colonias del pingüino de penacho amarillo en Isla Marion en lo que respecta a: (a) el número de parejas reproductoras, y (b) el éxito de la reproducción en el Río Van den Boogaard, Hoyo Trypot y Falla Trypot, 1983/84–2004/05.
- Figura 6: Comparación del número de parejas del pingüino de penacho Amarillo que se reproducen en el Río Van den Boogaard y en el Hoyo Trypot. Desde 1995/96 ha habido menos de 70 parejas reproductoras en el Hoyo Trypot y están disminuyendo.
- Figura 7: Tendencias del peso de los pingüinos de penacho amarillo en Isla Marion para: (a) machos al arribo a la colonia de reproducción, (b) hembras al arribo a la colonia de reproducción, y (c) polluelos al emplumecer, 1994/95–2004/05. Se muestra el promedio, la desviación estándar y el rango para cada temporada.