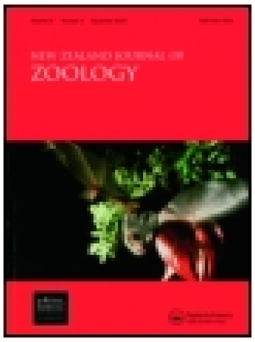

New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzz20

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To cite this article: Hiltrun Ratz , John T. Darby , Kerri-Anne Edge & Caryn Thompson (2004) Survival and breeding of yellow-eyed penguins (Megadyptes antipodes), at two locations on Otago Peninsula, South Island, New Zealand, 1991–96, New Zealand Journal of Zoology, 31:2, 133-147, DOI: 10.1080/03014223.2004.9518367

To link to this article: http://dx.doi.org/10.1080/03014223.2004.9518367

Published online: 30 Mar 2010.

New Zealand Journal of Zoology, 2004, Vol. 31: 133–147 133
0301–4223/04/3102–0133

Survival and breeding of yellow-eyed penguins (*Megadyptes antipodes*), at two locations on Otago Peninsula, South Island, New Zealand, 1991–96

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Abstract Two breeding locations of the endangered yellow-eyed penguin (*Megadyptes antipodes*), were monitored for six seasons between 1991 and 1996 to assess breeding success, breeding frequency, and survival parameters. Breeding success was inversely related to the total number of nests, suggesting that an influx of inexperienced breeders decreases the average breeding success. The proportions of males not breeding at either location in a season ranged from 0 to 13%, and 0 and 23% for females. Between 75 and 92% of breeders were recorded breeding in two consecutive seasons, while between 0 and 6% of breeders skipped one season and 9% of females (but no males) skipped two consecutive seasons. Annual survival averaged 90% for both breeding locations for four seasons (males 93%, females 90%).

Z03028; Online publication date 12 May 2004
Received 6 June 2003; accepted 30 January 2004

Keywords yellow-eyed penguin; life history parameters; breeding success; breeding frequency; skipping breeding seasons; annual survival

INTRODUCTION

The IUCN Red List category for yellow-eyed penguins (*Megadyptes antipodes*), a species endemic to the southern New Zealand region, has recently been upgraded from vulnerable (Collar & Crosby 1994) to endangered, based on a number of criteria: ongoing degradation of breeding habitat, predation of chicks by introduced predators (stoats (*Mustela erminea*), ferrets (*M. furo*), and feral cats (*Felis catus*)), and extreme fluctuations in numbers of individuals (population 4000) (BirdLife International 2000). Population fluctuations are due to food shortages at sea caused by sea temperature changes, drowning in fishing nets, accidental fires at breeding sites, and possibly avian malaria (BirdLife International 2000). Population parameters such as breeding success, frequency of breeding, and survival of breeding adults are important components of any future population modelling efforts to assess the conservation issues facing this species.

Otago Peninsula (46°S, 171°E) supports one of the highest concentrations of yellow-eyed penguins (Marchant & Higgins 1990) in its range. There have been no published records of detailed breeding success over several seasons since the 1986/87 breeding season (Darby & Seddon 1990). Intensive monitoring was instigated at two breeding locations on Otago Peninsula, and the habitat protection associated with a private ecotourism venture at Penguin Place included trapping of introduced predators (stoats, ferrets, and cats), provision of nest boxes, and extensive re-vegetation (Ratz & Thompson 1999). Breeding success is reduced when eggs fail to hatch and chicks die from starvation, problems in the nest, and introduced predators (Darby & Seddon 1990; Ratz & Murphy 1999). Hatching success and chick survival can further be reduced by a large increase in recruitment of young pairs or individuals, because penguins breeding for the first time have lower breeding success than experienced breeders (Richdale 1957; Ainley et al. 1983; Dann & Cullen 1990; Marchant & Higgins 1990; Williams 1995). The same is true in other long-lived seabirds (for example, Rowley 1983; Nol & Smith 1987; Bradley et al. 1990). Therefore, an increase in a breeding population may produce a decrease in average breeding success.

Nest site fidelity has been reported in most penguin species (Williams 1995), and breeding location fidelity is assumed to be the same as nest site fidelity if the latter is close to 100%. However, studies reporting lower nest site fidelity do not specify whether birds that fail to return to the nest site used previously also fail to return into the breeding location or colony (for example, Ainley & DeMaster 1980; Williams 1996; Pledger & Bullen 1998). Breeding location fidelity is very high in penguin species for whom this has been reported, for example, king penguins (*Aptenodytes patagonicus*) 100% (Weimerskirch et al. 1985); gentoo penguin (*Pygoscelis papua*) 100% (Williams & Rodwell 1992), but 73% in Trivelpiece & Trivelpiece (1990); Adélie penguins (*P. adeliae*), 99.9% for females, 100% for males (Trivelpiece & Trivelpiece 1990); and chinstrap penguins (*P. antarctica*) 99% (Trivelpiece & Trivelpiece 1990; Williams 1995). Yellow-eyed penguins are sedentary and tend to return faithfully to the breeding location where they have bred before (Richdale 1957; Marchant & Higgins 1990). In his study only 2% of breeders moved from their breeding locations (calculated from table 68 in Richdale 1957). The fidelity of breeding adults in returning to the breeding location (as opposed to the nest site) has direct implications for recording breeding frequency and survival rate.

Forty-eight percent of yellow-eyed penguin females start breeding aged 2 years, 48% aged 3 years, and 4% aged 4 years resulting with all females breeding thereafter (Richdale 1957). Males rarely start breeding aged 2 years (8%), more often at 3 years (47%) or 4 years (33%) (Richdale 1957). Fourteen percent of males did not breed for at least one season after the first attempt (Richdale 1957). With this knowledge it is possible to evaluate the proportion of individuals breeding each season, as well as survival.

The first long-term analysis of the survival of breeding adults referred to the seasons between 1936/38 and 1953/54: 87.7% a year (range 80–96%) for male and 84.5% a year (range 81–92%) for females (Richdale 1957, table 69). Edge et al. (1999) reported 91.3 and 90.3% survival of breeding adult yellow-eyed penguins in 1992 and 1993 respectively.

This study investigated the breeding success and survival of yellow-eyed penguins at two breeding locations on Otago Peninsula during the six breeding seasons from 1991/92 to 1996/97. The aims of this paper are to link fluctuating numbers of breeding pairs with breeding success, and to estimate the proportion and sex of breeders that skip one or two seasons.

STUDY LOCATIONS

The two breeding locations, Pipikaretu Beach (45°48′S, 170°45′E) and Ryans Beach (45°49′S, 170°45′E) are located near the tip of Otago Peninsula, South Island, New Zealand (Ratz & Thompson 1999). Pipikaretu Beach has a 500-m-long beach facing north-east, and Ryans Beach has a 550-m-long beach facing east. The area of each breeding location is about 5 ha and is flanked by cliffs. The sites are 500 m apart and separated by a headland. Both beaches are abutted by consolidated dunes either of bare sand or covered with pasture grasses, marram grass (*Ammophila arenaria*) and isolated patches of vines (*Muellenbeckia*), shrubs, and small trees. Nests are spread through these dunes, and wooden nest boxes were deployed to supplement the small amount of vegetation suitable for nest sites. The northern third of Pipikaretu Beach is used by commercial tour groups viewing the penguins from observation hides accessed through covered tunnels (Ratz & Thompson 1999).

METHODS

Breeding success

Nest searches were conducted at the two breeding locations on the following dates: 22 September 1991, 27 September 1992, 18 September 1993, 30 October 1994, 19 September 1995, and 26 September 1996. Subsequently, all nests were visited twice weekly and the contents of the nest recorded, except during hatching in 1992/93, 1993/94, and 1994/95 when they were checked daily as part of the manipulation study (Edge et al. 1999). For definitions of terms see Table 1.

The cause of chick deaths is not always clear. Chicks which disappear could have been taken by a predator, or could also lie squashed in the bottom of the nest. It is not always possible to find any remains of the dead chick in the nest even after the parents

Table 1 Definitions of terms.

Terms	Definitions
Tables 2 and 3	
Nests	A nest bowl containing at least one egg and at least one adult.
Chicks not fledged	
Found dead	All chicks found dead in or near the nest without obvious wounds or injuries that were often emaciated.
Disappeared	All chicks that could not be found. These may have been depredated but could also be missed.
Depredated	All chicks found dead with wounds presumably inflicted by a mammalian predator.
Chicks fledged	All chicks that were banded in early February. They were assumed to have fledged if they reached this age although fledging itself was not documented.
Hatching success	Percent of laid eggs that hatched.
Fledging success	Percent of hatched eggs that fledged chicks.
Reproductive success	Percent of laid eggs that fledged chicks.
Number of chicks/nest	The number of chicks fledged per nest.
Nest success	Percent of nests that fledged at least one chick.
Table 5	
Breeders	Adults breeding in a season.
Former breeders	Adults that bred in the past but were recorded alive and not breeding in a season.
Percentage of breeders	The number of breeders per total number of breeders and former breeders known to be alive in a season.
Table 6	
Breeders breeding in both seasons	Percent of breeders in the second season divided by the total number of breeders from Table 5 in the first season.
Table 7	
Skipping one season	A penguin breeding in season x, not breeding in season $x + 1$, but breeding in season $x + 2$.
Skipping two seasons	A penguin breeding in season x, not breeding in season $x + 1$ and $x + 2$, but breeding in season $x + 3$.
Table 8	
Annual survival rate	Percent of individuals alive in the second season divided by the number of individuals (breeders and former breeders) alive in the first season (from Table 5).

and potential siblings have moved out of the original nest bowl (see also Ratz & Murphy 1999). Fledged chicks that disappeared can be assumed to have been taken by predators, but they may have just been hiding exceptionally well. Other chicks that were found with bite marks were categorised as "preyed on"; the real cause of death could have been starvation or exposure and the wounds inflicted post-mortem (Ratz et al. 1999). Predation can be assigned as a cause of death with absolute certainty only when the event has been personally observed or captured on film (Ratz et al. 1999).

Seasons with manipulations

In the seasons 1992/93, 1993/94, and 1994/95, Pipikaretu Beach and Ryans Beach were used as part of an artificial brood reduction experiment by Edge et al. (1999). Eggs and chicks were added, removed or shifted within and between Pipikaretu Beach and Ryans Beach and other breeding locations. The eight nests on Pipikaretu Beach and seven nests on Ryans affected by these manipulations were excluded from the breeding success data and analyses.

Marking

Identification of individuals through banding is needed to assess breeding frequency and survival. Extensive banding in this study was started only in the 1992/93 season and continued in later years as new birds were recruited into the breeding population. All breeding adults were banded with a numbered stainless steel band on the right flipper. All birds were measured at the time of banding to estimate their sex (Darby & Seddon 1990). All chicks were banded in early February prior to fledging.

Statistical analyses

Hatching success, fledging success and reproductive success were compared between breeding locations and season using a logistic regression model (Z-test). Additionally, the regression model was used to test for differences between the sexes for the proportion of all penguins breeding, skipping seasons, and survival. A Fisher's exact test was also used in cases when the Z-test was not valid because of small sample sizes, and when the logistic regression models suggested an interaction between season and location. The 1991/92 and 1992/93 seasons were excluded from some statistical analyses detailed below, because of the small sample size of banded breeders in the former, and because almost all breeders were banded in the latter and therefore former breeders were unknown.

RESULTS

Breeding success

At both Pipikaretu Beach and Ryans Beach there were small annual fluctuations of 0–5 nests during the first four seasons of study, followed by more substantial increases of 5–9 nests per season for the final two seasons (Tables 2 and 3).

The average hatching success was 85.06% at Pipikaretu Beach (range 76–95%) and 85.14% (range 75–100%) at Ryans Beach (Tables 2 and 3) (Diff in –2 Log L = 0.001, d.f. = 5, $P = 0.980$). Hatching success varied between seasons (Diff in –2 Log L = 17.3982, d.f. = 5, $P = 0.0038$), and this variation differed between breeding locations (Diff in –2 Log L = 12.0829, d.f. = 5, $P = 0.0337$). However, hatching success was significantly different between the two colonies only in the 1992/93 season (Table 4).

The average fledging success during the six breeding seasons was 76.0% at Pipikaretu Beach (Table 2), and 83.0% at Ryans Beach (Table 3). This difference was not significant at the 95% confidence level (Diff in –2 Log L = 3.5852, d.f. = 5, $P = 0.0583$). Logistic regression models showed highly significant annual variation in fledging success (Diff in –2 Log L = 33.2517, d.f. = 5, $P < 0.0001$), and a significant relationship between breeding season and location (Diff in –2 Log L = 12.4557, d.f. = 5, $P = 0.0290$). However, fledging success was significantly different between the two colonies only in the 1994/95 and 1996/97 seasons (Table 4).

The average reproductive success was 64.6% at Pipikaretu Beach (Table 2) and 70.7% at Ryans Beach (Table 3), a difference that was not statistically significant (Diff in –2 Log L = 2.3183, d.f. = 1, $P = 0.1279$). Logistic regression models suggested a strong relationship between breeding season and location (Diff in –2 Log L = 20.0223, d.f. = 5, $P = 0.0012$). There was a high degree of annual variation in reproductive success (Diff in –2 Log L = 42.7821, d.f. = 5, $P < 0.0001$), and this was significant for the 1992/93, 1994/95, and 1996/97 seasons (Table 4).

The average number of chicks fledged per nest was 1.0 chicks per nest, or greater (maximum 1.9), at both locations in all years (Tables 2 and 3).

Breeding success was inversely related to total number of nests (Fig. 1). The correlation between the number of nests and the proportion of successful nests through the six consecutive seasons was significant for Pipikaretu Beach and for the two breeding locations combined, but not for Ryans Beach

Table 2 The breeding success of yellow-eyed penguins (*Megadyptes antipodes*) at Pipikaretu Beach, 1991–96. For definitions of the parameters see Table 1.

No.	1991/92	1992/93	1993/94	1994/95	1995/96	1996/97	Total
Nests	24	21	19	24	32	37	157
Eggs laid	47	42	38	45	63	73	308
Nests with two eggs	23	21	19	21	31	36	151
Nests with one egg	1	0	0	3	1	1	6
Eggs failed to hatch	7	2	2	6	15	14	46
Eggs hatched	40	40	36	39	48	59	262
Hatching success (%)	85.1	95.2	94.7	86.7	76.2	80.8	85.1
Chicks found dead	3	7	3	7	17	16	53
Chicks disappeared	0	0	0	0	0	3	3
Chicks depredated	0	0	0	3	0	4	7
Chicks fledged	37	33	33	29	31	36	199
Fledging success (%)	92.5	82.5	91.7	74.4	64.6	61.0	76.0
Reproductive success (%)	78.7	78.6	86.8	64.4	49.2	49.3	64.6
Chicks/nest	1.54	1.57	1.74	1.21	0.97	0.97	1.27
Standard deviation of chicks/nests	0.78	0.75	0.65	0.72	0.90	0.84	0.84
Nest success (%)	83.3	85.7	89.5	83.3	59.4	62.2	74.5
Nests failed at egg stage	2	0	1	2	4	3	12
Nests failed at chick stage	2	3	1	2	9	11	28

Table 3 The breeding success of yellow-eyed penguins (*Megadyptes antipodes*) at Ryans Beach, 1991–96. For definitions of parameters see Table 1.

No.	1991/92	1992/93	1993/94	1994/95	1995/96	1996/97	Total
Nests	18	18	16	17	25	34	128
Eggs laid	36	36	32	33	48	64	249
Nests with two eggs	18	18	16	16	23	30	121
Nests with one egg	0	0	0	1	2	4	7
Eggs failed to hatch	9	8	0	2	7	11	37
Eggs hatched	27	28	32	31	41	53	212
Hatching success (%)	75.0	77.8	100.0	93.9	85.4	82.8	85.1
Chicks found dead	3	5	1	1	14	8	32
Chicks disappeared	0	0	0	0	0	1	1
Chicks depredated	0	3	0	0	0	0	3
Chicks fledged	24	20	31	30	27	44	176
Fledging success (%)	88.9	71.4	96.9	96.8	65.9	83.0	83.0
Reproductive success (%)	66.7	55.6	96.9	90.9	56.3	68.8	70.7
Chicks/nest	1.33	1.11	1.94	1.76	1.08	1.29	1.38
Standard deviation of chicks/nests	0.84	0.83	0.25	0.56	0.91	0.84	0.82
Nest success (%)	77.8	88.9	100.0	94.1	64.0	76.5	81.3
Nests failed at egg stage	2	0	0	0	1	3	6
Nests failed at chick stage	2	2	0	1	8	5	18

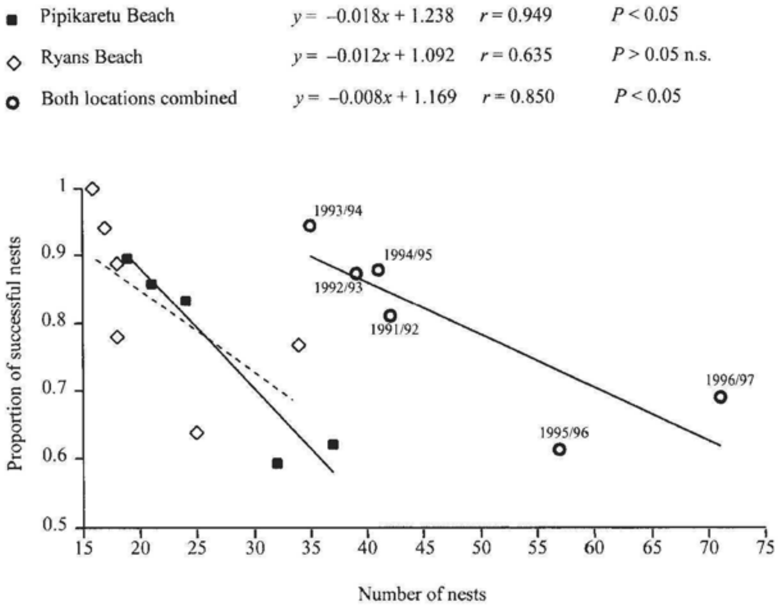


Fig. 1 The correlation between the proportion of successful nests and the number of nests for six consecutive seasons (1991/92 to 1996/97) for Pipikaretu Beach and Ryans Beach (dashed line) separately and both locations combined.

Table 4 Results of the *Z*-test and Fisher's exact test used to compare hatching success, fledging success, and reproductive success between the two locations in individual seasons. Asterisks (*) indicate statistical significance at 0.05 level.

Season	*Z*	*P* value	Fisher's exact test *P* value
Hatching success			
1991/92	1.16	0.247	
1992/93	2.30	0.21	0.038*
1993/94	–1.32	0.188	0.4965
1994/95	–1.05	0.296	0.4557
1995/96	–1.21	0.227	
1996/97	–0.30	0.763	
Fledging success			
1991/92	0.51	0.612	0.6786
1992/93	1.08	0.279	
1993/94	–0.91	0.362	0.6163
1994/95	–2.56	0.010	0.0176*
1995/96	–0.13	0.900	
1996/97	–2.57	0.010*	
Reproductive success			
1991/92	1.23	0.217	
1992/93	2.17	0.030*	
1993/94	–1.49	0.135	0.2088
1994/95	–2.69	0.001	0.0080*
1995/96	–0.74	0.462	
1996/97	–2.30	0.021*	

alone (Fig. 1). A "partial" correlation coefficient was $r = -0.738$, $P = 0.006$. This represents the strength of the relationship between the proportion of successful nests and number of nests after adjusting for any breeding location effect.

The correlation between hatching success, fledging success and reproductive success, and nest numbers was significant for Pipikaretu Beach but not for Ryans Beach nor for both locations combined (Fig. 2, 3, and 4).

Seasons with manipulations

At Pipikaretu Beach, two nests were manipulated in 1992/93: 1 egg was added, a total of 5 eggs failed to hatch, 4 chicks were added and 7 chicks died resulting in 37 chicks fledged. In 1993/94, four nests were manipulated: 2 eggs added, 3 eggs failed to hatch, 2 chicks added, 2 chicks transferred away, and 3 chicks died resulting in 37 chicks fledged. In 1994/95, two nests were manipulated: 1 egg was added, 9 eggs failed to hatch, 8 chicks were found dead, and 3 chicks were depredated resulting in 30 chicks fledged. Also, in the 1994/95 season, two eggs from one pair were transferred to a pair without eggs resulting in 27 breeding pairs but only 26 nests.

At Ryans Beach, four nests were manipulated in 1992/93: 3 eggs were added, a total of 11 eggs did not hatch, 2 chicks were added, 8 chicks were found dead, and 4 chicks were depredated, resulting in 25 chicks fledged. No nests were manipulated in 1993/94. In 1994/95, two nests were manipulated: 1 egg was added, 3 eggs failed to hatch, and 1 chick died

Fig. 2 The correlation between the mean hatching success and number of nests for six consecutive seasons (1991/92 to 1996/97) for Pipikaretu Beach and Ryans Beach (dashed line) separately and both locations combined.

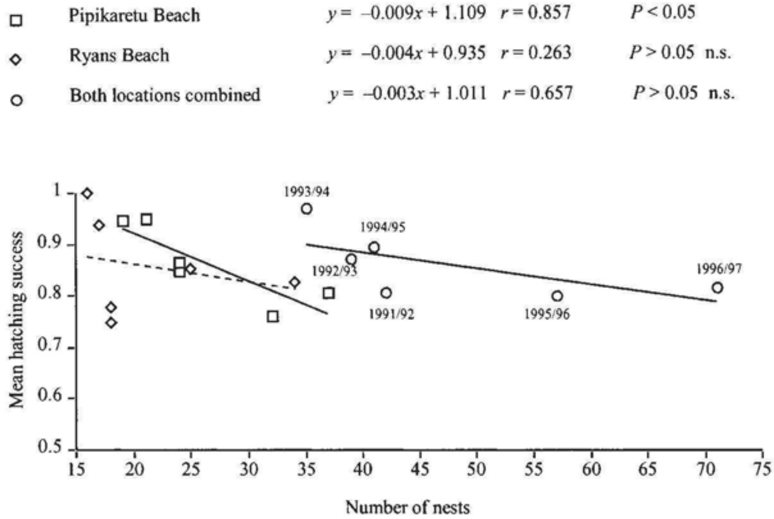
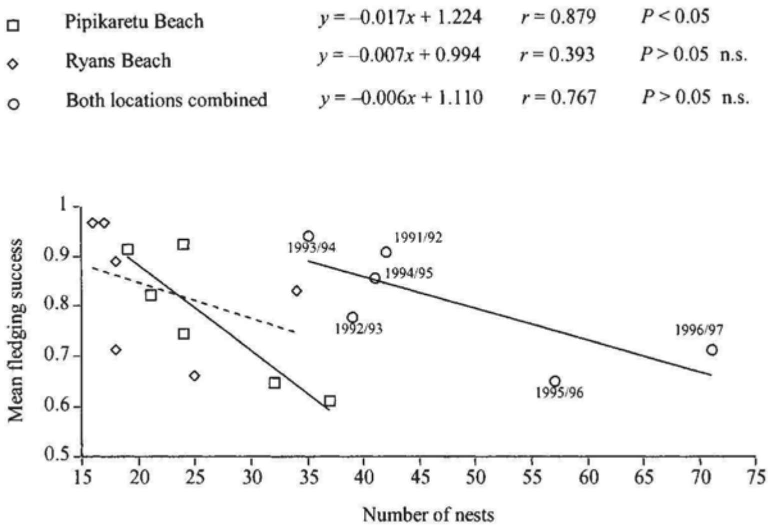


Fig. 3 The correlation between the mean fledging success and number of nests for six consecutive seasons (1991/92 to 1996/97) for Pipikaretu Beach and Ryans Beach (dashed line) separately and both locations combined.



resulting in 33 chicks fledged. Also, in the 1994/95 season, two eggs were transferred between two nests within Ryans Beach resulting in 20 breeding pairs but only 19 nests.

Proportion of breeders breeding

At Pipikaretu Beach on average 6% (range 4–10%) were recorded as former breeders, and 5% (range 1–16%) at Ryans Beach (Table 5). There was no significant difference of the proportion of breeders between the two locations (Diff in $-2 \log L = 0.0524$, d.f. = 1, $P = 0.8189$) and no significant difference between the breeding seasons and the locations (Diff in $-2 \log L = 3.027$, d.f. = 1, $P = 0.0819$). However, there was a significant increase in the proportion of all birds breeding over the four seasons (Diff in $-2 \operatorname{Log} L = 4.5076$, d.f. = 1, $P = 0.0337$).

All seasons combined, on average, 8.5% (range 5–13%) and 2.7% (range 0–15%) of males did not breed at Pipikaretu Beach and Ryans Beach, respectively, and 5.7% (range 5–8%) for both locations combined (Table 5). On average, 3.6% (range 0–10%) and 10.1% (range 5–23%) of females did not breed at Pipikaretu Beach and Ryans respectively,

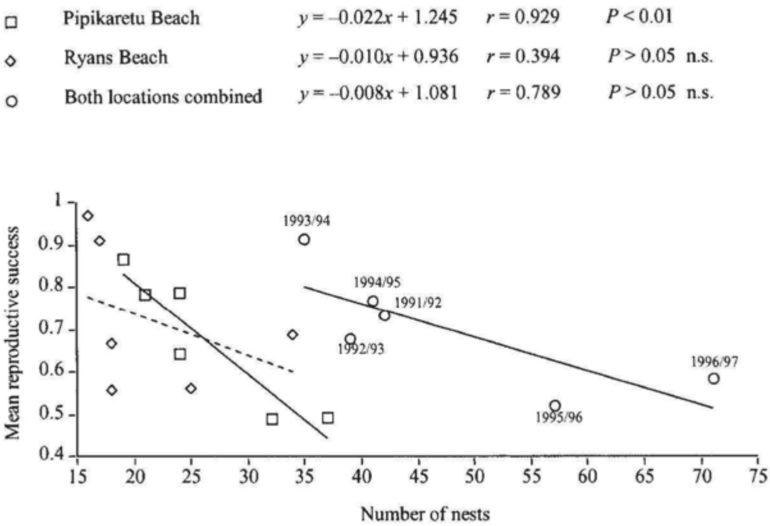


Fig. 4 The correlation between the mean reproductive success (chicks fledged per eggs laid) and number of nests for six consecutive seasons (1991/92 to 1996/97) for Pipikaretu Beach and Ryans Beach (dashed line) separately and both locations combined.

Table 5 The number and proportion of banded yellow-eyed penguins (*Megadyptes antipodes*) that were breeders or former breeders at Pipikaretu Beach and Ryans Beach, 1991–97. For definitions of terms see Table 1. The first two seasons (in italics) were not included in statistics because banding did not start until the 1992/93 season and former breeders could not be identified. The sexes were separated into males, females and unknown sex (?) in brackets.

	Pipikaretu Beach		Ryans Beach		Total	
Season	Breeders n (% of total) (male, female, ?)	Former breeders n (male, female, ?)	Breeders n (% of total) (male, female, ?)	Former breeders n (male, female, ?)	Breeders n (% of total) (male, female, ?)	Former breeders n (male, female, ?)
1991/92	*3 (–) (2,0,1)*	–	*4 (–) (2,2,0)*	–	*7 (–) (4,2,1)*	–
1992/93	*42 (–) (21,21,0)*	–	*31 (–) (16,15,0)*	–	*73 (–) (37,36,0)*	–
1993/94	44 (96) (22,22,0)	2 (1,1,0)	26 (84) (13,13,0)	5 (2,3,0)	70 (91) (35,35,0)	7 (2,4,0)
1994/95	45 (90) (23,21,1)	5 (3,2,0)	36 (95) (17,17,2)	2 (0,2,0)	81 (92) (40,38,3)	7 (3,4,0)
1995/96	59 (94) (29,28,2)	4 (3,1,0)	46 (96) (19,20,7)	2 (0,2,0)	105 (95) (48,48,9)	6 (3,3,0)
1996/97	73 (96) (36,37,0)	3 (3,0,0)	66 (99) (22,21,23)	1 (0,1,0)	139 (97) (59,57,23)	4 (3,1,0)

and 6.3% (range 2–11%) for both locations combined (Table 5). Considering males and females separately, none of the following were significant: the annual variation in breeding proportion for females (Diff in –2 Log L = 2.8934, d.f. = 1, P = 0.0889) and males (Diff in –2 Log L = 0.2413, d.f. = 1, P = 0.6232); the difference between the two locations for females (Diff in –2 Log L = 2.7794, d.f. = 1, P = 0.0955) and for males (Diff in –2 Log L = 0.9189, d.f. = 1, P = 0.3378); and the relationship between seasons and breeding locations for females (Diff in –2 Log L = 0.023, d.f. = 1, P = 0.8795) and for males (Diff in –2 Log L = 1.717, d.f. = 1, P = 0.1901).

Breeding in consecutive seasons

On average, 14% (range 7–22%) and 12% (range 8–19%) of male breeders did not breed in two consecutive seasons at Pipikaretu Beach and Ryans Beach respectively, 13% (range 8–18%) for both locations combined (Table 6). The difference between males and females breeding was not statistically significant for this parameter (Diff in –2 Log L = 0.742, d.f. = 1, P = 0.389). On average 10% (range 4–14%) and 26% (range 15–41%) of female breeders did not breed in two consecutive seasons at Pipikaretu Beach and Ryans Beach respectively, 17% (range 13–26%) for both locations combined (Table 6).

On average, 87% (range 80–92%) and 80% (range 75–88%) of breeders were breeding in two consecutive seasons at Pipikaretu Beach and Ryans Beach respectively, and 84% (range 83–90%) for both locations combined (Table 6). In the pooled data for males and females, there is no relationship between season and breeding location (Diff in –2 Log L = 2.4, d.f. = 3, P = 0.4936). There is also no annual difference between breeding locations (Diff in –2 Log L = 4.341, d.f. = 3, P = 0.2269). There was no significant difference in proportion of birds breeding in successive seasons (Diff in –2 Log L = 3.139, d.f. = 1, P = 0.0764).

Table 6 The number of banded yellow-eyed penguins (*Megadyptes antipodes*) bred in two consecutive seasons at Pipikaretu Beach and Ryans Beach, 1991–96. For definitions see Table 1. The first two seasons (in italics) were not included in statistics because banding did not start until the 1992/93 season and former breeders could not be identified. The sexes were separated into males, females and unknown sex (?) in brackets.

Seasons (x and x + 1)	Breeders breeding in both seasons n (% of total in season x – see Table 5) (male, female, ?) Pipikaretu	Ryans	Total
1991/92 & 1992/93	*2 (67)*	*4 (100)*	*6 (100)*
	(2,0,0)	*(2,2,0)*	*(4,2,0)*
1992/93 & 1993/94	37 (88)	25 (81)	62 (90)
	(18,19,0)	(13,12,0)	(31,31,0)
1993/94 & 1994/95	38 (86)	23 (88)	61 (84)
	(19,19,0)	(12,11,0)	(31,30,0)
1994/95 & 1995/96	36 (80)	27 (75)	63 (83)
	(18,18,0)	(15,10,2)	(33,28,2)
1995/96 & 1996/97	54 (92)	36 (78)	90 (86)
	(27,27,0)	(17,15,4)	(44,42,4)

Skipping of seasons

Pooling locations and both sexes, between 0 and 6% of breeders skipped one season (Table 7). On average 6% (range 0–13%) and 0% of male breeders skipped one season at Pipikaretu Beach and Ryans Beach respectively, and 4% (range 0–8%) for both locations combined (Table 7). On average 3% (range 0–6%) and 14% (range 13–17%) of female breeders skipped one season at Pipikaretu Beach and Ryans Beach respectively, and 6% (range 5–8%) for both locations combined (Table 7). Difference between locations, sexes, and over sets of seasons could not be tested because the sample sizes are too small, and the parameter estimates in the logistic regression model are unstable and perhaps unreliable (due to the zero values in the first set of seasons).

Skipping of two consecutive seasons (1993/94 and 1994/95) was recorded twice (all females) in the set of four seasons from 1992/93 to 1995/96.

Table 7 The number of banded yellow-eyed penguins (*Megadyptes antipodes*) that were breeding at Pipikaretu Beach (Pipi) and Ryans Beach in three consecutive seasons and the number and proportion of total breeders that did not breed in the middle season. The sexes were separated into males, females, and unknown sex (?) in brackets.

		1992/93 1993/94 1994/95		1993/94 1994/95 1995/96		1994/95 1995/96 1996/97	
Number of breeders breeding in all three seasons n (male, female, ?)	Pipi	33	(16,17,0)	31	(15,16,0)	34	(16,18,0)
	Ryans	23	(12,11,0)	17	(11,6,0)	23	(14,8,1)
	Total	56	(28,28,0)	48	(26,22,0)	57	(30,26,1)
Number of breeders NOT breeding in the 2nd of three seasons; n (male, female, ?)	Pipi	0 (0%)		2 (6%)	(2,0,0)	1 (3%)	(0,1,0)
	Ryans	0 (0%)		1 (6%)	(0,1,0)	1 (4%)	(0,1,0)
	Total	0 (0%)		3 (6%)	(2,1,0)	2 (4%)	(0,2,0)

Table 8 Annual survival of banded yellow-eyed penguins (*Megadyptes antipodes*) that bred at Pipikaretu Beach and Ryans Beach, 1991–96. The first two seasons (in italics) were not included in statistics because banding did not start until the 1992/93 season and former breeders could not be identified. The sexes were separated into males, females, and unknown sex (?) in brackets.

	Number and proportion of birds surviving in consecutive seasons (male, female, ?)					
	Pipikaretu		Ryans		Total	
Consecutive seasons	Season *n*	Season +1 *n* (%)	Season *n*	Season +1 *n* (%)	Season *n*	Season +1 *n* (%)
1991/92 & 1992/93	*3*	*2 (67)* *(2,0,0)*	*4*	*4 (100)* *(2,2,0)*	*7*	*6 (86)* *(4,2,0)*
1992/93 & 1993/94	42	39 (93) (19,20,0)	31	30 (97) (15,15,0)	73	69 (95) (34,35,0)
1993/94 & 1994/95	46	44 (96) (23,21,0)	31	29 (94) (14,15,0)	77	73 (95) (37,36,0)
1994/95 & 1995/96	50	45 (90) (24,21,0)	38	31 (82) (15,14,2)	88	76 (86) (39,35,2)
1995/96 & 1996/97	63	58 (92) (30,28,0)	48	38 (79) (17,17,4)	111	96 (86) (47,45,4)

One of 15 females (none of the 13 males) at Pipikaretu Beach and one of 6 females (none of 11 males) at Ryans Beach skipped the middle two seasons. In the set of four seasons from 1993/94 to 1996/97, at Pipikaretu Beach 14 males and 16 females and 10 males and 4 females at Ryans Beach bred all four seasons, but none were observed to skip both middle seasons. No statistical analyses to test for location, sex or set of seasons effects were valid with such small sample sizes.

Banding and adult survival

In the 1991/92 season only seven breeding adults had bands and could be identified at Pipikaretu Beach and Ryans Beach (Table 5). The annual survival at both locations combined was 86% (six of the seven) between 1991/92 and 1992/93. This was based on a small sample of banded adults (Table 8); this survival rate is ignored for all statistical analyses, even though it is still within the range recorded for the other seasons (Table 8).

The average annual survival at Pipikaretu Beach was 92.5% (range 86–93%) and 86.5% (range 79–97%) at Ryans Beach, and 90.0% (range 86–95%) for both locations combined (Table 8). Annual survival rate over the period 1992–96 did not change (Diff in –2 Log L = 4.311, d.f. = 3, $P = 0.2298$). There is no evidence of a difference in survival rate between the two locations (Diff in –2 Log L = 3.743, d.f. = 1, $P = 0.053$).

The average survival for males was 94.1% (range 90–100%) and 89.6% (range 88–94%) for Pipikaretu Beach and Ryans Beach respectively, and 92.9% (range 91–100%) for both locations combined (Table 8). The average survival for females was 93.8% (range 91–97%) and 84.7% (range 74–100%) for Pipikaretu Beach and Ryans Beach respectively, and 89.9% (range 83–97%) for both locations combined (Table 8). There is no statistical difference in survival rates between the sexes (Diff in –2 Log L = 0.863, d.f. = 1, $P = 0.3529$).

DISCUSSION

Survival

The only published long-term study of survival rate for breeding yellow-eyed penguins was reported by Richdale (1957, table 72) over 15 years (the first season was excluded due to low sample size): 85.6% with a range of 73.7– 94.2%. The average survival rate of 90% (range 86–95%) measured in this study was higher, albeit over a short time frame of 4 years, than found by Richdale (1957). We found no statistically significant annual variation in survival or between the two breeding locations, and although the survival rate of females was 3% lower on average than that for males, this was also not significantly different. Richdale (1957, table 69) also reported a lower survival rate for females (84.5%) than males (87.7%). Edge et al. (1999) reported 91.3 and 90.3% breeding adult survival of yellow-eyed penguins in 1992 and 1993 respectively.

Gentoo penguins weigh about the same as yellow-eyed penguins (5–6 kg) and start breeding at a minimum of 2 years, raise two chicks and have an annual survival of 86.5% (Marchant & Higgins 1990; Jouventin & Weimerskirch 1991). The gentoo penguin survival rate is similar to that reported by Richdale (1957) for yellow-eyed penguins but lower than recorded here. Adélie penguins also breed annually, fledge a maximum of two chicks and are similar in body weight to yellow-eyed penguins, and they had an annual survival rate of 78.6% in 1969/70 and 61.4% in 1975/76 (Ainley & deMaster 1980). This low survival compared with yellow-eyed penguins was attributed to harsher winter conditions for Adélie penguins, their longer travel distances for feeding, and higher predation (Ainley & DeMaster 1980). Low adult survival rates of breeding adults must be offset by a higher average reproductive output if a stable population is to be maintained in the long term.

Survival can be affected by age and/or breeding status. Annual survival was independent of age for 6 to 13-year-old Adélie penguins, but survival of breeding females increased with age while that of non-breeding females stayed the same (Ainley & DeMaster 1980). Survival of breeding males also increased with age while that of non-breeding males decreased with age (Ainley & DeMaster 1980).

Breeding Adélie penguins are subject to a higher predation risk by leopard seals (*Hydrurga leptonyx*), whom they have to pass on their way to and from the breeding rookery many more times than non-breeding adults, to relieve the mate and/or feed the chicks (Ainley & DeMaster 1980). Non-breeding individuals pass less often and are in better condition because they don't have to feed and then return quickly (Ainley & DeMaster 1980). This leads to a skewed sex ratio, favouring males, among the older birds in the colony (Ainley & De Master 1980). Richdale (1957) reported a less pronounced male sex bias for yellow-eyed penguins. Ainley & DeMaster (1980) concluded that breeding at a young age is not as costly for yellow-eyed penguins as for Adélie penguins, and that the mortality factors operate at greater intensity on Adélie penguins. Predation of Adélie penguins by seals has been estimated between 2.3 and 7.3% (Ainley & DeMaster 1980).

There are no comparable estimates for predation at sea on yellow-eyed penguins, although the occasional predation by New Zealand sea lions (*Phocarctos hookeri*) has been observed from shore or inferred from injuries (Ainley & DeMaster 1980; Moore & Moffat 1992; Schweigman & Darby 1997; Ratz & Thompson 1999; C. Lalas pers. comm.; H. McGrouther pers. comm.; H. Ratz pers. obs.). The chance of encountering a sea lion is greater near the shore (Richdale 1957; Darby & Seddon 1990; Marchant & Higgins 1990). Breeding Adélie penguins come ashore more often than non-breeding individuals, while yellow-eyed penguin breeding and non-breeding adults come ashore mostly daily throughout the year (Richdale 1957; Darby & Seddon 1990; Marchant & Higgins 1990). However, New Zealand sea lions are rare in South Island waters (Lalas 1997; McConkey et al. 2002) and so is predation of penguins (C. Lalas pers. comm.). Other predators are difficult if not impossible to identify, but barracouta (*Thyrsites atun*) can inflict potentially fatal wounds on the feet and lower abdomen (H. Ratz pers. obs.), and various shark species are present in the inshore waters. Therefore, all yellow-eyed penguins are equally at risk of predation by sea lions and have a similar survival rate, while breeding Adélie penguins are exposed to a much higher predation risk by leopard seals than non-breeding adults who have a higher survival rate.

There was an unusually high mortality of adults in summer 1989/90 on the Otago Peninsula (Gill & Darby 1993) which was attributed to avian malaria (Graczyk et al. 1995). A further cause of increased mortality in some years could be reduced availability of food (van Heezik & Davis 1990), possibly related to climate conditions such as El Niño-Southern Oscillation events (Peacock et al. 2000). The low mortality observed during this study compared with that found by Richdale (1957) indicates that the climate and food supply were probably favourable in 1991–97.

Breeding parameters

Hatching success averaged 85% over the reported six breeding seasons in this study, a level of success similar to other studies: 84.7% (six seasons, 1981/82–1986/87) Otago Peninsula (Darby & Seddon 1990); 78% (16 seasons, 1936/37–1952/53) Otago Peninsula (Richdale 1957); 87% (three seasons, 1991/92–1993/94) Catlins (Ratz & Murphy 1999); 85% (three seasons, 1992/93–1994/95) Otago Peninsula (Edge et al. 1999); 83% (one season, 1987/88) Campbell Island (Moore 1992). The gentoo penguin is the ecological equivalent to the yellow-eyed penguin: it is mostly sedentary (Bost & Jouventin 1990;

Marchant & Higgins 1990); has low inter-nest distances (Bost & Jouventin 1990; Marchant & Higgins 1990); it lays two eggs (Williams 1980) and often raises two chicks (Croxall & Prince 1980; Marchant & Higgins 1990); parents change over at the nest about every 24 h; and they forage close to shore (Croxall & Prince 1980; Trivelpiece et al. 1987; Marchant & Higgins 1990) and at similar depths to yellow-eyed penguins (Conroy & Twelves 1972; Seddon & van Heezik 1990). The hatching success of the gentoo penguin is 90% (one season, 1976/77) on Bird Island (Croxall & Prince 1979), 67% on South Shetland Island (nine seasons, 1976/77–1985/86) (Trivelpiece et al. 1987) and 61% on Possession Island (three seasons, 1983/84–1985/86) (Bost & Jouventin 1991). Blue penguins, sympatric with yellow-eyed penguins, have had reported a variable hatching success of 40–81% (seven seasons, 1992–98) (Perriman & Steen 2000) and 51–63% in New Zealand (two seasons, 1995–96) (Bull 2000) and its close relative the little penguin in Australia has a hatching success of 64% in Victoria (11 seasons, 1968–78) (Reilly & Cullen 1981), or 61–100% on Bowen Island (three seasons, 1987/88–1989/90) (Fortescue 1995). Therefore, the hatching success of yellow-eyed penguins is similar to that of the ecologically similar gentoo penguins and the sympatric blue penguin.

The number of chicks fledged per nest by gentoo penguins varied between 0.36 and 1.14 in the four colonies studied on Macquarie Island in 1978/79 (Reilly & Kerle 1981) and 0.46 on Crozet Island from 1983–88 (Bost & Jouventin 1991). Blue penguins fledged 0.94 chicks per nest on Matiu-Somes Island, Wellington, New Zealand, in 1995–97 (Bull 2000), or 58–96% of chicks fledged at Taiaroa Head, Otago, New Zealand, in 1992–98 (Perriman & Steen 2000), or on average 41% of little blue penguin chicks were fledged in Victoria, Australia, between 1968 and 1978 (Reilly & Cullen 1981), or 69–100% of hatched chicks fledged on Bowen Island, Australia, between 1987/88 and 1989/90 (Fortescue 1995). Although fledging success was variable between locations and seasons, both species appear to fledge fewer chicks on average than yellow-eyed penguins.

Breeding success of yellow-eyed penguins at the Otago Peninsula from 1981/82 to 1986/87 (Darby & Seddon 1990) was similar to our study at Pipikaretu Beach and Ryans Beach from 1991/92 to 1996/97. Hatching success or fertility decreased when the number of nests increased in both studies (except in the 1981/82 and 1982/83 seasons when both increased (Darby & Seddon 1990)). Richdale (1957) reported the number of eggs laid, hatched, and chicks reared for 16 years in the 1930s and 1940s. In 53% of seasons there the hatching success decreased after an increase in eggs laid, success increased in 20% of seasons after the number of eggs laid decreased, while both success and egg numbers increased or decreased (both 13% of seasons) (Richdale 1957). Richdale (1957) also reported a lower hatching success of eggs laid by first time breeders, so an increase in nest numbers indicates an influx of first-time breeders, and caused a corresponding decrease in the overall hatching success. Relatively low hatching success coincided with an almost doubling of nest numbers in another breeding location on the Otago Peninsula in the mid 1990s, and was also attributed to the low fertility of first time breeders (McKay et al. 1999).

Fledging success did not show such a clear correlation with nest numbers in this study. Darby & Seddon (1990) recorded a steady increase in fledging success with increasing nest numbers (three consecutive seasons) and then a fall in fledging success with a decrease in nest numbers (two consecutive seasons). In 47% of seasons, the number of chicks fledged per nest increased with an increase in nest numbers in five breeding locations between 1991/92 and 1994/95 (Moore 1999). In 13% of seasons an increase in nest numbers followed a decrease in the number of chicks fledged per nest, while a decrease in nest numbers was followed by a decrease (20% of seasons) or an increase (20% of seasons) in number of chicks fledged per nest (Moore 1999). In Richdale's (1957) study, fledging success increased as often as it decreased after an increase in number of eggs laid (both 33% of seasons), and fledging success decreased (in 13% of seasons) and increased (in 20% of seasons) after number of eggs laid decreased. The lowest number of chicks fledged per nest for seven seasons was recorded after an almost doubling of nest numbers in 1995/96 (McKay et al. 1999).

Food availability influences chick survival (van Heezik & Davis 1990; Moore & Wakelin 1997) and therefore can disrupt any clear relationships between nest numbers and fledging success depending on adult experience. Climatic variables such as rain, air, and sea surface temperature influence nest numbers, the number of eggs laid and hatched, and the number of chicks fledged by yellow-eyed penguins on the Otago Peninsula, but the details of these interactions are unclear (Peacock et al. 2000). Their analysis of Richdale's (1957) data from the 1930s and 1940s suggested that fledging success and survival declined in cold and wet conditions, yet both increased during the 1980s under similar conditions (Peacock et al. 2000). The suggested link between climate and the penguin population is ocean productivity, and for some population parameters there may be a time lag after changes to the climate (Peacock et al. 2000).

Breeding success can further be influenced by factors ashore such as nesting habitat. Peacock et al. (2000) suggested that the decrease in the population variables during hot and dry seasons in the 1980s was caused by deforestation of coastal breeding habitat and the associated heat stress for breeding penguins. However, although nests in grassland had a lower hatching rate than those in shrubland, this was attributed to a large increase in nest numbers and hence in first time breeders with lower hatching success, rather than heat stress (McKay et al. 1999).

Breeding frequency

Yellow-eyed penguins have a high fidelity to their breeding locations (Richdale 1957; Marchant & Higgins 1990). Only 2% of breeders have been recorded in a different breeding location after starting to breed (calculated from table 68 in Richdale 1957). Their breeding habitat can include dense vegetation in which it is hard to locate all nests; for example, in one study 5% of nests were not discovered until after chicks hatched (Ratz & Murphy 1999). However, in our study areas there was minimal vegetation and many nest sites were artificial boxes, hence we assumed that all nests were located and other adults present were skipping that season (see Methods).

Our study showed that both males and females can skip one season or two. Some males perhaps could not find a mate because of the higher mortality of females (Richdale 1957; Ainley & DeMaster 1980). Another possibility is that a mate died very close to the time of egg laying and the remaining adult was unable to find a new mate in time. Young breeders have a higher mortality than older ones, but the surviving young breeders generally have a higher lifetime reproductive output than older ones that delayed the onset of breeding and which were also more likely to skip a season later in life (Ainley & DeMaster 1980).

Twenty-five percent of gentoo penguins and 14% of macaroni penguins (*Eudyptes chrysolophus*) did not breed on Bird Island, South Georgia, between 1986 and 1987, perhaps because of frequent food shortages (Williams & Rodwell 1992). Boersma (1998) also reported reduced breeding activity of Galapagos penguins (*Spheniscus mendiculus*) in years of low food availability. At Ryans Beach a number of yellow-eyed penguins skipped breeding in 1994/95 and 1995/96 but only in the latter season was fledging success lower than in other seasons (Table 3). Although various factors affect fledging success, it might be an evolutionary advantage for birds to be able to predict a season with a low food supply or to cease breeding when conditions become poor. Low food supply can result in underweight chicks with corresponding low fledging rates (van Heezik & Davis 1990; Bost & Jouventin 1991). Lack of food may also deplete fat reserves of the adults, resulting in starvation or death during the annual moult that follows breeding (van Heezik & Davis 1990). On the other hand, the proportion of individuals in the population that skip a season is much lower than that recorded for gentoo penguins and macaroni penguins (Williams & Rodwell 1992).

CONCLUSION

Survival rates, reproductive output and frequency of breeding over a number of seasons are parameters that can be used to assess the viability of a population. This paper has provided values for life history parameters of yellow-eyed penguins from one part of the Otago Peninsula, which could contribute to future population modelling of this endangered species. However, the factors influencing all of these parameters are numerous and they interact in ways poorly understood. Reproductive success and survival in yellow-eyed penguins are influenced by the El Niño Southern Oscillation (ENSO) phenomenon and its associated effect on food supply (van Heezik & Davis 1990; Peacock et al. 2000). Therefore, to assess the stability and the reproductive output of populations, breeding data need to be collected for many seasons. The present study covered six seasons for breeding success and four seasons for survival during a period of increase in nest numbers, so the means recorded may not be representative. Long-term records are required for a more accurate assessment of average values for population parameters and trends. The contribution of climate, availability of nesting habitat, seasonal variability of food supply, the impact of predators, and age distribution of breeders requires modelling to assess the importance of each factor. For this, close monitoring of a number of colonies over a number of seasons is essential. Although much is known about this species, there are still significant gaps in our knowledge and hence our ability to prevent the (localised) extinction of this rare penguin.

ACKNOWLEDGMENTS

This study has been conducted as part of the monitoring programme at "Penguin Place", a private ecotourism venture that finances conservation work at Pipikaretu Beach and Ryans Beach. Thanks are due to the owners, Howard and Elizabeth McGrouther, Scott Clarke, and Barbara Morrison, for their far-sightedness in protecting and closely monitoring these penguins. Special thanks to Dr Chris Lalas for comments on the manuscript and many productive discussions. Thanks also to the two referees and the editor for their input that much improved this manuscript.

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