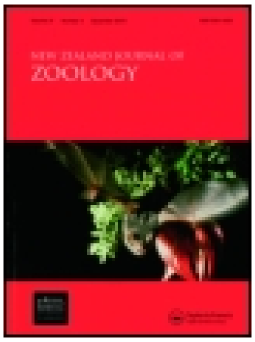

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Seasonal variation in survival, weights, and population counts of blue penguins (Eudyptula minor) in Otago, New Zealand

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Seasonal variation in survival, weights, and population counts of blue penguins (*Eudyptula Minor*) in Otago, New Zealand

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Abstract To estimate the cost of moulting on blue penguin survival we conducted a 17-month mark recapture study. We used a round-up trap set at sunset to catch penguins returning from the sea to their burrows. Survival and density were modelled using capture-recapture models. We found that survival was lower in the post-moult months compared with the rest of the year. No mortality was found during the period from egg laying to chick fledging. The peak of the breeding season was the time when the population size could be estimated most accurately. However, 3 trapping nights seems to be too low for reliable population size estimation. From a subsample of the captured penguins we found weights similar to those recorded previously for this species in Otago.

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INTRODUCTION

Penguins are unusual among birds in that they renew the whole plumage annually over a short period (Williams 1995) during which time they cannot forage. As for most penguin species, blue penguins moult after the end of the breeding season (Reilly & Cullen 1983) spending 2–3 weeks fasting on land, surviving on their fat reserves (Stahel & Gales 1987). An individual penguins' condition after moult will depend on the amount of fat it gained prior to moult (Williams et al. 1992). Among dead birds recovered there is a peak of starved, newly moulted adults in the months following moult (Reilly & Cullen 1979; Dann et al. 1992), suggesting that some penguins' body condition is critically poor during and after the moult. However, period-specific peaks in dead recoveries can reflect higher colony attendance, or other factors that lead to a higher probability of finding a bird once it was dead, rather than a peak in mortality. Accounting for period-specific recapture or recovery probabilities is therefore important when testing for survival differences in different periods of the year. Demographic parameters and population size estimates for blue penguins are usually obtained by nest monitoring. These data can be hard to obtain when penguins nest in deep burrows.

At some sites, blue penguins returning to shore at dusk come ashore in groups using the same path (Klomp & Wooller 1991), making recaptures possible before they reach their nests. To test if penguin survival was lower in the period after moult compared with other times of the year we trapped penguins returning from sea at Pilots Beach, Otago, New Zealand, 3 days each month for 17 months. This period covered two breeding seasons and one moult period. We estimated survival using open capture-recapture models and population sizes using closed capture-recapture models (Pollock et al. 1990).

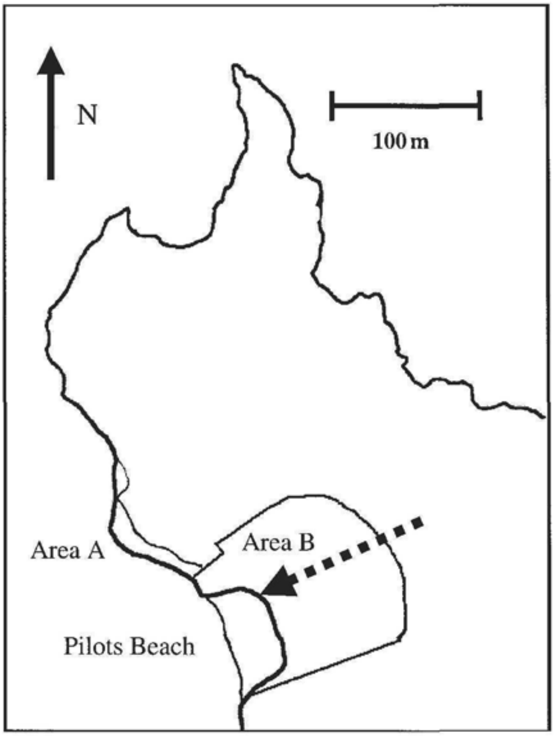

Fig. 1 Taiaroa Head, Otago Peninsula, with Pilots Beach, Area A and Area B. Broken arrow points to the location of the round-up trap.

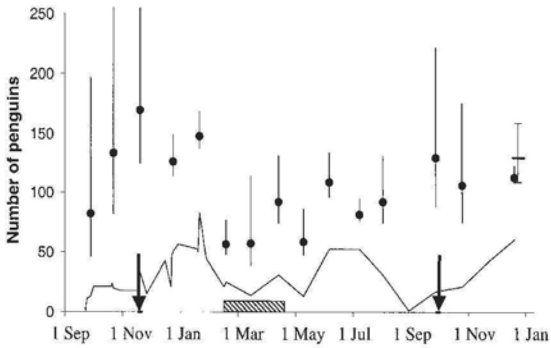

Fig. 2 The line shows no. of trapped penguins in the trapping period. When the trapping occurred 3 nights in a row the no. of birds trapped on the first night is shown. Closed circles = population sizes with confidence intervals. August and November 2000 trap sessions lack population size estimates due to few captures (Aug) and disturbance during trapping (Nov). The December 2000 density estimate was done based on 4 nights trapping and population size estimated using a Jacknife estimator (bar). Same estimator used for the other periods (closed circles). Down arrows indicate the average egg laying date in the adjacent colony Area A; the hatched area indicates the moulting season.

METHODS

Study area and penguin monitoring

The study area is situated at Taiaroa Head, Otago Peninsula, New Zealand (Fig. 1). In Area A (Fig. 1) breeding performance of the blue penguins has been monitored intensively since 1992 (Perriman 1997; Perriman & Steen 2000).

Penguins returning at dusk to their burrows in Area B come ashore on Pilots Beach and use one single access path up the steep slope from the beach. We used a "round-up trap" (a corral made of nylon mesh fence) at the end of the access path to capture penguins. The trap was erected before sunset and we withdrew from the pen until dusk when we could hear and see the penguins coming ashore. We then carefully herded the penguins from the beach up the path and into the corral. The penguins usually came ashore in one or two main groups. We handled the first group before we herded the second group into the trap. One hour after the arrival of the first group, the round-up trap was removed and the trapping session ended.

The round-up trap was used irregularly from June 1993 until the start of this study in September 1999. From 22 September 1999 until 21 December 2000 (end of the study, 49 trapping periods) we trapped 3 days a month according to Pollock's robust design (Pollock et al. 1990) allowing density and survival estimation. To increase precision we trapped for 4 nights on the last trapping period (18–21 December 2000). In addition, we trapped 1 night per week from early September 1999 until mid-January 2000. Upon capture, flipper band number and sex, according to subjective visual judgement of the shape and size of the beak, was recorded (Stahel & Gales 1987). Unbanded penguins were banded. Upon banding, the depth and the length of the beak were measured using callipers. A subsample of the penguins was weighed upon capture (usually the first 15–20 penguins).

Data and statistical analysis

Population estimates and survival

We estimated population size by using closed capture-recapture models implemented in the program MARK (White & Burnham 1999) using the trap histories from the monthly 3-day trapping. We trapped 4 nights in December 2000 allowing us to use the Jacknife estimator for closed populations implemented in the program CAPTURE (Pollock et al. 1990) for this period. The Jacknife method allows for heterogeneity in recapture probability among animals, and gives a more reliable density estimate.

We used the program MARK option robust to estimate survival, taking into account temporal unavailability of capture (Kendall et al. 1997). We divided the year into five biological periods that we think affects the penguins differently, i.e., midwinter, early breeding, late breeding, moult, and post moult periods (e.g., Stahel & Gales 1987; Gales & Green 1990). The actual dates for the different periods are given in Table 1. We used the likelihood ratio test (LRT) to evaluate if specific effects were statistically significant (Burnham & Anderson 1992).

Weights

The first 15–20 birds were weighed to the nearest 10 g using an electronic balance. When a bird was captured more than once during a month, the average weight for that bird in that month was used.

Sexing of birds

Sex is most reliably determined for breeding birds by using auxiliary information such as the body and beak size of the partner and sexual behaviour together with beak measurements (Renner & Davis 1999). However, we had to rely entirely on beak measurements and subjective judgement of beak shape and size to sex birds (Stahel & Gales 1987; Gales 1988; Hocken & Russell 2002). We had beak measurements for 68% of the captured penguins. According to the criterion developed by Hocken & Russell (2002) for Otago blue penguins, 60% of our sample were classified as females. The skewed sex ratio is possibly due to juvenile males without fully-grown beaks being classified as females (Gales 1987; Hocken & Russell 2002). Therefore, birds that were banded less than a year before they were captured during the current study were excluded to avoid juveniles. Also, the birds with the smallest beaks at banding were checked for the sex recorded later in the study and some were reclassified since their beaks were not fully grown at first sex determination. Using this method, 55% of the birds with beak measurements %re eventually classified as females.

RESULTS

Population size estimation

We caught 268 different penguins during the study. Of these, 258 were banded at Taiaroa Head or Pilots Beach, and one was banded at Penguin Beach (c. 2 km away). Nine birds were banded in Oamaru (80 km north), but these nine birds were each only observed once. They might be either short-term visitors to the colony, or their bands were misread, so they were not included in the data for the population size estimation. Only 13% of the birds caught were banded as chicks and could therefore be properly aged.

Table 1 Eight-week survival of blue penguins at Taiaroa Head. Periods correspond to different phases of reproduction and moulting and the 95% confidence intervals. –, indicates that the standard errors were not estimable. Yearly average 8-week survival is 0.95 (0.91; 0.97).

Dates	Periods	Period-specific survival	95% CI
22 Sep–22 Dec 1999	Early breeding season	1	–
22 Dec 1999–16 Feb 2000	Late breeding season	1	–
16 Feb–12 Apr 2000	Moult	0.91	0.68; 0.98
12 Apr–7 Jun 2000	Post-moult	0.88	0.70; 0.96
7 Jun–2 Aug 2000	Midwinter	0.94	0.59; 0.99
2 Aug–27 Sep 2000	Early breeding season	1	–
27 Sep–20 Dec 2000	Late breeding season	1	–

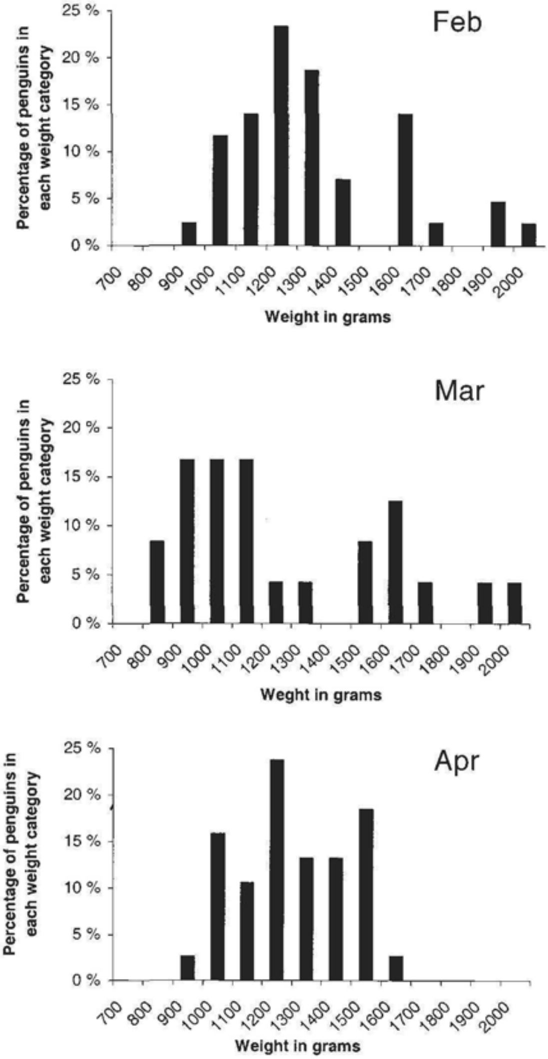

Fig. 3 Percentage of birds in different weight categories. In February and March, the weight distribution was bimodal because there are birds in both post-moulting and pre-moulting condition. This blurs the effect of the moult on individual weight. In April all birds had finished moult so we regarded the penguins as one homogeneous group.

The number of captured penguins in the round-up trap and the population size estimates for the periods with 3 consecutive trap nights is shown in Fig. 2. There was a significant difference in trapping probability in the different trapping periods (LRT, $\chi^2 = 30.1$, $P = 0.005$, d.f. = 14). The trapping probability was highest in midsummer (December both years, January and February 2000), and midwinter (July 2000) and lowest in spring (October and September both years, Table 2).

Table 2 Probability of capturing a penguin given it is alive. Probability of capture was different between the months, and higher on the first day of a trap session than on the 2 consecutive days. Due to poor data, capture probability for November 2000 could not be estimated.

	First day		Second/third day	
Trap session	Estimate	SE	Estimate	SE
21–23 Sep 1999	0.16	0.05	0.13	0.10
19–21 Oct 1999	0.16	0.07	0.12	0.12
16–18 Nov 1999	0.22	0.04	0.17	0.08
21–23 Dec 1999	0.45	0.04	0.38	0.08
18–20 Jan 2000	0.50	0.04	0.43	0.07
15–17 Feb 2000	0.42	0.06	0.35	0.12
15–17 Mar 2000	0.23	0.08	0.18	0.14
13–15 Apr 2000	0.32	0.05	0.26	0.10
10–12 May 2000	0.36	0.07	0.29	0.12
6–8 Jun 2000	0.42	0.04	0.35	0.09
8–10 Jul 2000	0.56	0.04	0.49	0.08
2–4 Aug 2000	0.32	0.05	0.26	0.10
27–29 Sep 2000	0.20	0.05	0.15	0.09
25–27 Oct 2000	0.23	0.06	0.18	0.10
22–23 Nov 2000	NA		NA	
19–21 Dec 2000	0.54	0.03	0.46	0.06

The trapping probability was higher the first night compared with the next 2 nights of trapping within a trapping period (Table 2, LRT, $\chi^2 = 6.8$, $P = 0.009$, d.f. = 1).

The estimated population size for December 2000 using the Jacknife estimator allowing for heterogeneity was higher than the estimate using the estimator with different trapping probability in the first and the next trapping days and no heterogeneity (Fig. 2), and had wider confidence intervals. According to the model selection criterion in the program CAPTURE, the Jacknife estimator was the best estimator for the December 2000 trapping period.

Survival

Due to sparse data in some of the trapping periods (Fig. 2), we had to exclude some of the capture occasions to estimate survival using the robust design model in program MARK. Therefore, we estimated survival rates from only seven periods (see Table 1). We excluded birds banded during the study period because these individuals might be subadult birds. Birds captured only once were also excluded, since these birds' bands were probably misread or they were not residents. Of the 268 penguins caught,

Table 3 Average weight in grams with sample size and standard errors for male and female blue penguins. Sample sizes for males and females do not add up to the total because only penguins with beak measurements that showed they were at least 1-year-of-age when weighed were included in the sex-specific weights.

		Female			Male			Pooled		
Year	Month	Weight	SE	*n*	Weight	SE	*n*	Weight	SE	*N*
1999	Sep	1122	33	18	1302	43	20	1197	24	58
	Oct	1190	26	34	1226	28	28	1173	17	86
	Nov	1222	19	40	1311	21	22	1222	13	91
	Dec	1285	47	10	1401	49	14	1324	32	31
2000	Jan	1181	40	3	1185	82	6	1199	37	15
	Feb	1214	44	18	1308	93	8	1255	40	43
	Mar	1100	103	12	1217	150	7	1181	73	24
	Apr	1145	30	20	1276	61	13	1207	28	42
	May	1188	40	16	1302	44	13	1249	27	39
	Jun	1154	29	21	1221	31	17	1197	17	51
	Jul	1246	30	22	1333	37	15	1263	20	53
	Aug	1116	25	22	1207	33	20	1160	18	54
	Sep	1266	28	19	1258	32	21	1252	19	55
	Oct	1206	25	19	1266	33	17	1239	17	51
	Nov	NA								
	Dec	1272	47	10	1381	72	7	1304	28	25

the survival analysis includes only 174 birds thought to be resident adult breeders in the population.

We found that in the breeding season, survival was equal to 1, i.e., a boundary estimate with no error estimable (Table 1). Survival during moult, post-moulting, and midwinter was significantly lower than the yearly average ($\chi^2 = 7.02$, $P = 0.03$, d.f. = 2), with the lowest survival in the post-moult period (Table 1).

Body weights

Monthly sex specific and pooled weights for all birds are shown in Table 3. The weights were similar to those reported for the species in Otago previously (Gales 1987). Blue penguins increase in weight at the onset of moult and decrease in weight after moult (e.g., Stahel & Gales 1987; Dann et al. 2000). This pattern can not be seen from Table 2, because the sample of birds in the months of moult consisted of a mixture of birds in post-moult and pre-moult condition (see Fig. 3).

DISCUSSION

There was a seasonal pattern in trappability of blue penguins at Pilots Beach that corresponds to the yearly life cycle of the blue penguins. Therefore, the density estimates from December (both years) and January (2000 only) had the most precise population estimates with narrowest confidence limits. This period corresponds to the time when most penguins had stopped guarding their chicks and both parents were foraging during the day and returning to feed the chicks at night (assuming that the average lay date in Area A corresponded to the lay date in Area B, which was 4 November 1999 and 5 October 2000). The high number of penguins and the high trappability in midwinter 2000 (early July) probably corresponds to the courtship period. The low probability of capture and consequently low number of penguins caught in the spring of both years (August/September, Fig. 2) probably corresponds to the honeymoon period that follows courtship and precedes egg laying (Stahel & Gales 1987; Chiaradia 2000).

The consistent tendency towards lower capture probability on the 2 nights following the first night of trapping possibly indicates a response to handling. However, there was no difference in the probability of capture for a given bird on the second and third capture day depending on whether it had been captured the first night or not ($\chi^2 = 7.73$, $P = 0.46$, d.f. = 8). Since birds captured on the first day had the same capture probability on the second and third day as a bird not captured on the first day, it is therefore likely that recently trapped individuals influenced the group's behaviour by being more cautious, e.g., by making landfall later at night or staying at sea (Klomp & Wooller 1991; Chiaradia 2000).

Closed capture-recapture models, including heterogeneous probability of capture among individuals, could not be applied reliably with only 3 trap nights (Pollock et al. 1990). In the last trapping period (December 2000), we trapped for 4 consecutive nights and selected models to estimate capture probability with the program CAPTURE (Pollock et al. 1990). The best model included individual heterogeneity in capture probability. This model (Fig. 2) gave a higher estimated population size and wider confidence limits than the model including different trapping probability for the first and later trapping nights. This indicates that estimates of population size based on the models we used might be biased low, and that more than 3 nights should be used in future studies of this type.

We found highest survival in the breeding season and reduced survival in the periods around moult (mid-February to mid-March), in the post-moult period (mid-March–early June) and in midwinter (early June–early August). Our results for seasonal variation in mortality are consistent with findings from banding records from Australia, where the peak in recoveries of dead birds has been found in autumn–early spring. This coincides with the period of, or right after, the moult, and is outside the breeding season (Reilly & Cullen 1979; Stahel & Gales 1987; Dann et al. 1992; Harrigan 1992; Norman et al. 1992; Dann et al. 2000). We did not detect a second mortality peak in the pre-breeding season as seen in Australia.

The causes of higher mortality in these periods compared with low mortality in the breeding season are not known, although the proximate cause of death for recovered adult penguins that died at sea is starvation (Harrigan 1992). The energy demand during the breeding season is the highest for blue penguins (Gales & Green 1990), but midwinter (July) was the only period when Gales & Green (1990) found a negative energy balance. Lower temperatures and productivity at sea in winter might tip the energy balance in the winter months, and lead to increased mortality in this period (e.g., Golet et al. 1998). The extent to which the period from autumn until early spring constitutes a survival "bottle neck" will probably vary from year to year. In previous studies, high numbers of dead recoveries in winter were correlated with late onset of breeding and low breeding success in the following breeding season (Norman et al. 1992; Dann et al. 2000). Both the breeding season 1999 and 2000 had late onsets of breeding (but not particularly low fledgling success, Perriman unpubl. data) compared with the breeding seasons of 1992–1997 (Perriman et al. 2000), indicating that the winter mortality found in the present study might be somewhat higher than normal. The relationship between the onset of breeding and the Southern Oscillation Index (SOI) found by Perriman et al. (2000) for the breeding seasons 1992–1998, was not confirmed in the breeding seasons 1999 and 2000. The result of Perriman et al. (2000) was dependent on a late onset of breeding and high SOI in 1998 compared with the previous years (1992–1997). The tendency towards late onset of breeding has continued in both the 1999 and 2000 season, but the SOI index in 1999 and in 2000 was more normal.

To follow blue penguin populations on the mainland, where they are very susceptible to predation, population size and individual survival should be monitored (Dann 1992; Perriman & Steen 2000). Monitoring should preferably be done during the guard stage and courtship period when the penguins are the most trappable. In addition, many geographically separated colonies should be monitored to detect large-scale trends in population change caused by changes in the marine ecosystem (e.g., Bost & Le Maho 1993).

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