Population studies of yellow-eyed penguins

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CONTENTS

Abstract

Conservation of yellow-eyed penguins (*Megadyptes antipodes*) on the New Zealand mainland requires accurate data on population trend, annual variation in survival, and several other parameters that can be estimated from banding data. We describe initial analyses using a newly constructed database of yellow-eyed penguin breeding and banding data, maintained by Manaaki Whenua. All known banding records of fledglings, juveniles and adults (n = 5894, 1972-1994) are tabulated by year for 46 mainland breeding areas and three southern islands (Codfish, Enderby and Campbell). Annual survival and recruitment were analysed for the intensively studied Double Bay and Midsection areas on Otago Peninsula. Adult survival varied between 49% and 100% over the 1982/83 - 1992/93 period; excluding one year of extraordinarily high mortality (1989/90), the lowest annual adult survival rate was 80% in 1985/86 - 1986/87. The average adult survival rate (83 +/- 13%) did not differ significantly from that reported 45 years earlier. The proportion of banded fledglings resighted as adults varied between 1 % and 38% in different cohorts, and almost half were resighted at an area other than their natal area. Mark-recapture estimates of total adult population showed no recovery from the 1989-90 catastrophe by the 1992-93 breeding season.

We demonstrate that adult yellow-eyed penguins are likely to be male when the sum of head length and foot length exceeds 269 mm. The 14% error rate by this criterion may be further reduced to about 2% by measuring both birds of a definitely mated heterosexual pair and considering the larger to be the male. The proportion of adult-aged birds breeding in any year was extremely variable (30% - 90%); care must therefore be taken when applying Richdale's "60%" rule of thumb for extrapolating the total population from the number of nests. We are unable to estimate separately the non-breeding rates of males and females as prior to 1992 relatively few adults were measured for sexing. We propose a new system of paper record forms for use by field workers.

1. Introduction

The yellow-eyed penguin (*Megadyptes antipodes*) is a large and distinctive species restricted to southern New Zealand, including Auckland and Campbell Islands (Darby & Seddon 1990; Marchant & Higgins 1990). Loss of breeding habitat and recent population declines in remaining areas have raised doubts about the long-term persistence of South Island breeding populations.

Funding was provided by the Science and Research Division and Otago Conservancy of the Department of Conservation in 1992-93 for Manaaki Whenua - Landcare Research, Dunedin, to complete the first phase of development of a relational database of yellow-eyed penguin banding records. Work on the database began in 1989 with resources provided by DSIR Ecology

Division. This report records the completion of the objectives for 1993-94 and describes analyses of annual survival using the database. As a database is of limited value without background information on how the data were collected, we include some notes on data collection and other relevant background in a section on Field Methods.

2. Background

Yellow-eyed penguins have become the focus of considerable conservation efforts by the Department of Conservation as well as private individuals and groups. A Species Conservation Strategy was developed over several years and last revised in 1991 (Department of Conservation 1991). Various research projects are aimed at providing an improved scientific basis for management. Underlying all these is a need to understand the natural population dynamics of the species and how different management strategies might enhance the viability of mainland populations. Long-term banding records provide a means to assess conservation progress and to estimate parameters for population models that can be used to predict the results of alternative management scenarios.

Detailed descriptions of the biology of yellow-eyed penguins may be found in Darby & Seddon (1990) and Marchant & Higgins (1990). Seasonal biology is outlined here as background to the analyses of annual survival. Yellow-eyed penguins breed in coastal forest and scrub and on farmland along the south-east coast of the South Island, particularly on Otago Peninsula and in the Catlins. Two eggs are normally laid in late September and hatch 6-7 weeks later in November. Chicks reach adult weight in mid-late January and then moult to juvenile plumage before fledging in February-March. Juvenile plumage is retained until the autumn moult after the next breeding season. Females may breed during their first season in adult plumage when they reach 2 years old, males tend to start breeding somewhat older. Adults undertake only short (1-5 day) foraging trips away from the breeding areas throughout the year, but juveniles may be absent for several months.

The reproductive performance of Otago yellow-eyed penguins is relatively well documented for the seasons 1936-37 to 1953-54 (Richdale 1957) and 1981-82 to 1986-87 (Darby & Seddon 1990). Survival rates of adults and post-fledging survival of juveniles are more difficult to measure than chick productivity, but are at least as important in determining population trends. Richdale (1957) estimated survival of yellow-eyed penguins on the Otago Peninsula by the proportion of banded birds known to reappear in subsequent years (the "recovery rate"). Annual survival of adults (? 4 years old) estimated in this way averaged 85.6% over 1937-38 to 1953-54 (Richdale 1957: Table 72; range 74% -94%).

3. Objectives

To investigate annual variation in the survival of juvenile and adult penguins on Otago Peninsula as shown by banding and recovery data, and draft a paper with J. Darby for publication in a scientific journal.

To maintain a PC database of yellow-eyed penguin banding and recovery records, including (i) retrospective checking and correction as required (ii) entry and checking of banding and recovery data from 1993-94 season (iii) annotation of any significant modifications to the database after the initial report (iv) regular backup.

To advise on a system of paper record forms for use by field workers to improve and standardise data collection and to streamline future data handling. Also to convene a round-table discussion to sort out problems

To report on morphometric methods for sex discrimination in yellow-eyed penguins.

4. Methods

4.1 FIELD METHODS

Many yellow-eyed penguins have been banded during intensive studies of growth, feeding, breeding success, etc., over the last 20 years. Penguins were observed intensively at a few sites in each year, generally as a component of other studies (Appendix 10.1). Only near Boulder Beach, Otago Peninsula, has a population been monitored intensively for more than 4 consecutive years. Other data are from sites studied intensively for shorter periods or visited only occasionally, and from incidental records of birds away from breeding areas. Even at intensively studied sites, the proportion of birds that were banded varied between areas and between years as a result of the varying resources and aims of the contributing studies.

Almost all the mainland breeding areas referred to here were identified in a previous inventory of yellow-eyed penguin habitats (Seddon *et al.* 1989 unpubl.), where descriptions of vegetation and other site factors may be found. Grid references of all breeding areas are given in Efford *et al.* (1994, unpubl. Landcare Research contract report). The database also includes banding data from Campbell Island (Moore & Moffat 1990 unpubl DoC internal report; Moore 1991 unpubl. DoC internal report; D. Garrick pers. comm.; P. Moore pers. comm.), Enderby Island in the Auckland group (Darby & Seddon 1986), Codfish Island (R. Nilsson pers. comm.; A. Wright pers. comm.; Yvan Heezik pers. comm.; P. Moore pers. comm.; Dean Nelson pers. comm.) and Green Island (Otago; C. Lalas pers. comm.).

Pulli (young-of-the-year) were banded between mid January and early February when they were about to fledge. Adults were usually banded in September-November during late incubation or while guarding young. Recoveries (observations of previously banded birds) were also generally made when nests were checked during the breeding season (see below). Banded birds were occasionally found dead at other times and reported to the Banding Office or Otago Museum. Van Heezik (1988, 1990) also captured birds at landing places for diet sampling, but the residency and breeding status of these birds are unknown.

The presence of juveniles and non-breeding adults was not monitored consistently at any site, although non-breeders were reported sometimes.

detailed banding methods described below relate specifically to studies undertaken or supervised by J. Darby on Otago Peninsula.

The main study areas were visited 12-20 times each season. In the first 1-2 years of monitoring at any area, considerable effort went into searching for nests, using sign such as tracks in vegetation and across sand, guano, and observation of birds coming ashore in the evening. In later years, sampling was mostly based on the list of nests and birds known from the previous year. Considerable effort was expended looking for birds that did not appear at their previous year's nest site, including checking every site used in preceding years. The first nest searches were in early to mid September, with searches being repeated at 3-4 day intervals until mid-October. This effort was mostly directed at collecting information on laying dates, but all nest sites of the previous year were checked on each round to see if the birds had returned.

A few nests were missed in the early season searches, but were located when chicks were banded in late January. At this time the chicks were more vocal, nests smelled more in the heat, and the accumulating guano was highly visible. However, by late January many chicks had moved away from their original nest site, which therefore remained unknown.

Very few nests were missed by this protocol, but some adult breeders were nt identified because they were always at sea when nests were checked or moved off the nest when approached.

Birds were restrained in a cloth sleeve for banding, measurement, and weighing. Young chicks were sometimes web-tagged for individual identification from the early nestling stage. Birds were usually marked with a single stainless steel flipper band. Each band bore the prefix "J" and a 4 or 5-digit punched number. Bands were applied to the left flipper from 1973 to 1981, with the exception of a few birds banded by D. Garrick in 1980 on the right flipper (Darby 1986 unpubl., p. 31; cf Lalas 1985 unpubl.). Since 1981-82 all birds were banded on the right flipper. A small number of birds were banded on both flippers, either as part of a small trial to assess band loss (van Heezik unpubl. data) or to carry coloured tape for individual identification at a distaance (Darby & Edge 1993 unpubl.).

A new stainless steel band was introduced at the end of 1984 to replace the previous bands which were too small. The first batch of these had unacceptably sharp edges and aluminium bands were used in 1985-86 pending resupply of stainless steel bands (cf. Darby 1986 unpubl.). Chicks of that year were all given a common web-tag to aid identification if the aluminium band was lost. A modified stainless steel band was introduced in 1987 and has been used exclusively since then. The band was closed on the flipper with a pair of adjustable slip-jaw pliers. The facing edges of the band were overlapped by about 1 mm when first applied rather than abutted, to allow for the slight opening of the band over time. This generally resulted in the edges neatly abutting after a few months (if there is a gap, there is a risk of the band snagging on vegetation and rock edges).

Bands were replaced when they were worn, sprung open, or lost, and surviving aluminium bands were replaced with stainless steel bands when birds were relocated after 1986. Two adults caught for banding had marks from a previous band that Ad been lost.

Study populations were subject to a variety of interventions for management and research (Appendix 10.2).

4.2 DATA ENTRY AND CHECKING

A relational database of banding and nesting data was established in Paradox 4.0. The structure of the database is described in a separate report (Efford et al. 1994 unpubl. Landcare Research contract report). The database resides on a PC fileserver attached to a local area network at the Dunedin office of Manaaki - Whenua.

Records of first banding and rebanding were entered from the standard returns made to the Banding Office, mostly held by J. Darby. All known records of yellow-eyed penguins banded between January 1973 and March 1994 have now been entered and checked. Known applications of J-bands to yellow-eyed penguins were checked off against a list of the numbers 1 to 14000. Gaps in the record were queried with the Banding Office to determine whether the bands concerned had been issued, and whether they had been used for other species. Almost all bands that might have been used on yellow-eyed penguins have been accounted for, so we are confident that the banding records in the database are nearly complete.

Recovery information was obtained from a variety of sources, none complete in itself. The Banding Office provided us with a DBase file of reported recoveries, which formed the basis for the recovery table in the database for 1973-92, thereby avoiding a good deal of data entry. Later recovery data were entered directly from data provided by field workers. These data were comprehensively checked against breeding and recovery records held by J. Darby to fill in missing locality information and remove inconsistencies.

We had not planned to enter nesting data in this phase of the project, but this proved necessary because nest records were an essential source of information on annual recoveries of breeding birds and on pairings. We captured this information by creating a record in the table NEST for each known breeding attempt. The NEST record included the year, a code for the breeding area, a nest identifier, the identity of parents (if known), counts of eggs laid and hatched, chicks fledged, and the identities of any chicks banded at the nest. Other fields such as those for the estimated dates of laying and hatching are not completed at this stage.

The list of breeding areas in the habitat inventory of Seddon et al. (1989 unpubl. report) was revised, with the addition of metric grid references and precisely corresponding latitudes and longitudes obtained from the yard grid references using the programs GRDCON and LATCON (Guyon Warren ex Institute of Geological and Nuclear Sciences, Lower Hutt).

A protocol for annual batch update of the database was successfully tested using the data from the 1992-93 and 1993-94 breeding seasons (Efford et al. 1994 unpubl. Landcare Research contract report). Schedules of banding and recoveries for the New Zealand National Banding Scheme were printed from the database, rather than manually transcribed from the field data as in previous years.

New recording forms were developed in consultation with field workers and used in the 1993-94 breeding season. Only slight modifications were required for the 1994-95 season, mostly to accommodate additional codes for, e.g., the fate of chicks (Appendix 10.3).

4.3 POPULATION ANALYSIS

Adult population size (N) and annual survival rates (f) were estimated by the full Jolly-Seber method using the program JS (Efford 1991 unpubl. DSIR technical record). This statistical method is preferable to the use of raw "recovery rates" because it allows for the possibility that surviving animals are not immediately resighted (e.g., Seber 1982; Lebreton et al. 1992). The Jolly-Seber mark-recapture method makes a number of assumptions that are only partly met by these data, but the resulting downward bias in survival rates is likely to be small (e.g., Seber 1982; see also section 7.2). Disappearance rates were calculated as 1-f.

Double Bay and Mid-section near Boulder Beach, Otago Peninsula, were the only sizable breeding areas that had been monitored for more than 4 consecutive years. Estimates of annual survival are presented only for these areas, which were pooled to increase the sample size and reduce problems caused by the considerable movement of penguins between them. The analysis used data from the 1982-83 to 1993-94 breeding seasons. A bird was recorded as "captured" if it was recorded (banded, sighted, recovered dead, etc.) as an adult at any time within the breeding year in question (June - May).

4.4 SEXING FROM MEASUREMENTS

Male and female yellow-eyed penguins cannot be distinguished by plumage, and their body weights do not differ consistently throughout the year (Richdale 1951, 1957). Several authors have found that the sexes of other penguin species can be distinguished with fair reliability from linear measurements, particularly those of the head and bill (e.g., Gales 1988; Murie et al. 1988; Scolaro et al. 1983). Darby & Seddon (1990) reported successful discrimination using head and foot lengths for 86% of females. Here we provide more detailed analyses overlapping in part with those of Darby & Seddon.

Two measurements were used: head length (from the back of the foramen magnum to the tip of the bill) and length of the foot excluding the claw (from the back of the heel to the tip of the pad of the middle toe). These measurements were taken intermittently during the 1980s and more consistently since 1990-1, particularly on Otago Peninsula. Overall, 27.4% of adults recorded on Otago Peninsula were measured as adults (n=1196). Of the 479 adults recorded on Otago Peninsula during or after the 1990-91 season, 58.5% had been measured as adults and were therefore potentially able to be sexed from head and foot measurements.

Known-sex birds

To establish the sexing method it was necessary to have a calibration sample of measured adult birds whose sex was known. This sample came from a number of sources (Table 1). If a bird was measured more than once as an adult, only the first set of measurements was used in the analysis. All birds in the known-sex sample were from Otago Peninsula; only data before the 1993-94 season were used in these analyses.

TABLE 1 DETERMINATION OF THE SEX OF BANDED BIRDS WHICH WERE ALSO MEASURED AS ADULTS.

SOURCE/METHOD	MALES	FEMALES
Autopsied at Otago Museum	3	9
Bloody cloaca at laying	0	1
Egg palpated before laying	0	1
Attendance at nest during egg laying	0	16
Karotype determination (Seddon 1988)	2	0
Pairing with a bird of known sex	24	7
Total	29	34

' Seddon (1988) determined the sex of three pairs of birds from karyotypes, but we did not have individual measurements for four of these birds.

A further 26 adults and 15 juveniles sexed by autopsy were excluded from the known-sex calibration sample either because they were unbanded or because their measurements were not available in time for the analysis. These birds were used to test the accuracy of the sexing criterion.

Inference of sex from mates of known sex

Richdale (1951 p.109; 1957 p. 2) found that so many of his study birds changed mates that he could infer the sex of most birds in a breeding area from the sex of a few. Since few birds have been sexed directly in recent studies, at least in the period up to 1992, it seemed desirable to use pairing information to extrapolate the sex of their known partners. A "pairing network" was defined as a network of pair bonds linked by birds known to have re-mated. By knowing the sex of a single bird within a pairing network it is possible to infer the sex of all other members, assuming that all pairings are heterosexual and have been correctly identified. A program, "SEXNET", was written to ensure that pairing networks were consistently and completely identified from the data in the database.

5. Results

5.1 DATABASE ENTRY AND CHECKING

The database records the banding of 3790 pulli, 423 juveniles, and 1681 adults in the period 1972-1994. A full breakdown of banding by site and year is given in Appendix 10.4. Recoveries of dead birds accounted for 368 individuals (Appendix 10.5).

5.2 POPULATION ANALYSIS

Monitoring of the adult population was intensive at only a few sites. Recoveries of adults were tied heavily to nest monitoring, for example, 79.5 % of adult recoveries at Double Bay and Mid-section, Otago Peninsula, were of breeders (n = 1261; excluding resightings within a year). Intensive study sites and years were defined arbitrarily as those where more than five nests were monitored and more than 70% of the associated breeders were identified. These criteria were met from 1983-84 to 1993-94 at Double Bay and Mid-section, and for shorter periods elsewhere (Table 2).

Annual survival and population change

A total of 339 different banded adult penguins were recorded at Double Bay or Mid-section between 1982-83 and 1993-94. The numbers observed annually varied from 37 to 154; some of this variation was due to population change and some (particularly the low tally in 1982-83) to varying banding effort. Some (20.5%) records (n = 1261) were outside the breeding season or were not associated conclusively with a nest. Jolly-Seber estimates of population size varied between 94 and 169 over 1983-84 to 1992-93 (Fig. 1). Although these estimates are open to question because some assumptions were not met (Discussion) they suggest that between 53% and 96% of resident adults were identified in any year.

The number of adults (breeders and non-breeders) in the intensive study population declined by 20% from 1985-86 to 1987-88, but had recovered again by 1989-90. The adult population dropped by 36% between 1989-90 and 1990-91, and remained low until 1992-93, the latest season for which Jolly-Seber estimates could be calculated. The number of adults seen annually averaged 81% t 12% of the Jolly-Seber population estimate in 1983-1992. We can crudely estimate the adult population in 1993-94 by dividing the number of adults seen (n=105; 1993-94) by the previous average probability of sighting (0.81). This method gives an estimate of 130 for 1993-94, indicating significant recovery from the 1990 crash. Numbers of adults post-crash have otherwise averaged about 33% below pre-crash levels (1983-1989: 152 t 14; 1990-1992: 102 t 8). The Jolly-Seber "survival" rates, f, represent the probability of a bird remaining alive and in the local population until the following breeding season (Table .3).

TABLE 2 SUMMARY OF NEST MONITORING EFFORT AT MAJOR STUDY SITES. SHADING INDICATES AREAS AND YEARS IN WHICH MONITORING WAS CONSIDERED INTENSIVE (> 5 NESTS AND > 70% BREEDERS IDENTIFIED. "-" INDICATES NO DATA WERE COLLECTED.

a. Number of nests at which eggs known to have been laid

	Breeding area (see below for codes)									
Year	PA	SF	DB	MS	A1	HC	NP	OH	LP	Total
1982-83	19	-	31	20	4	13	-	-	-	87
1983-84	26	1	36	27	23	10	28	-	-	151
1984-85	30	-	39	31	6	33	29	-	-	168
1985-86	29	-	39	30	11	29	24	-	-	162
1986-87	28	-	27	19	-	17	-	-	-	91
1987-88	-	-	25	19	-	7	-	-	-	51
1988-89	-	-	28	24	-	10	20	4	-	86
1989-90	-	-	27	26	-	-	16	5	-	74
1990-91	-	9	9	7	10	9	3	7	7	61
1991-92	-	15	13	23	11	17	3	6	15	103
1992-93	-	15	13	19	11	16	8	7	32	121
1993-94	-	13	18	24	13	18	6	7	36	135
Total	132	53	305	269	89	179	137	36	90	1290

b. Percentage of breeders (2 x a) banded and identified

	Breeding area (see below for codes)									
Year	PA	SF	DB	MS	A1	HC	NP	OH	LP	Total
1982-83	16	-	2	3	0	4	-	-	-	5
1983-84	48	100	89	89	26	30	18	-	-	55
1984-85	97	-	85	100	17	71	14	-	-	72
1985-86	95	-	95	95	82	83	13	-	-	80
1986-87	95	-	91	100	-	91	-	-	-	94
1987-88	-	-	96	100	-	71	-	-	-	94
1988-89	-	-	98	92	-	0	43	13	-	68
1989-90	-	-	98	98	-	-	59	10	-	84
1990-91	-	83	89	100	75	78	67	100	86	85
1991-92	-	93	100	96	95	71	83	83	67	86
1992-93	-	100	100	95	100	94	100	100	92	96
1993-94	-	100	100	98	100	92	83	100	97	97
Total	75	95	84	89	65	68	35	75	89	76

Breeding areas

PA	Papanui Beach, Otago Peninsula
SF	Sandfly Bay, Otago Peninsula
DB	Double Bay, Otago Peninsula
MS	Mid-section, Boulder Beach, Otago Peninsula
A1	A1 section, Boulder Beach, Otago Peninsula
HC	Highcliff, Otago Peninsula
NP	Nugget Point, Catlins
OH	Owaka Heads, Catlins
LP	Long Point, Catlins

TABLE 3 MARK-RECAPTURE ANALYSIS FOR ADULT YELLOW-EYED PENGUINS AT DOUBLE BAY AND MID-SECTION, OTAGO PENINSULA, 1982-92. SEXES POOLED.
-" INDICATES ESTIMATES THAT COULD NOT BE CALCULATED.

	COUNTS FROM FIELD DATA			JOLLY-SEBER ESTIMATES					
YEAR	NUMBER SEEN	NEW	ALIVE, NOT SEEN[1]	ANNUAL SURVIVAL			POPULATION ESTIMATE		
				ϕ^2	s.e.	95% CI	N	s.e.	% SEEN[3]
1982-83	37	37[4]	0	0.854	0.062	(0.731-0.959)	-	-	-
1983-84	133	106	5	0.898	0.027	(0.843-0.949)	155.6	11.3	85
1984-85	150	31	4	0.897	0.028	(0.841-0.951)	155.5	1.6	96
1985-86	154	26	8	0.798	0.039	(0.721-0.882)	166.5	2.8	92
1986-87	108	13	29	0.818	0.041	(0.741-0.900)	149.1	4.9	72
1987-88	107	12	22	0.889	0.033	(0.824-0.952)	133.1	3.2	79
1988-89	122	19	11	1.000	0.056	(0.908-1.000)	136.8	2.4	89
1989-90	125	24	16	0.492	0.051	(0.397-0.615)	168.5	9.9	74
1990-91	58	16	30	0.837	0.054	(0.737-0.944)	108.2	7.8	54
1991-92	87	21	11	0.838	0.044	(0.752-0.924)	104.3	3.5	83
1992-93	77	8	13	-	-	-	93.7	2.5	82
1993-94	105	26	0	-	-		-	-	-

1. "Alive, not seen" includes birds banded before the year in question and not recorded in that year but seen afterwards. 2. ϕ is the estimated probability of surviving to the following year.
3. 100 x Number seen / Population estimate. 4. For the purposes of this analysis, all adults seen in 1982-83 were "new" although some had been banded previously.

Estimated survival was 80% or more in every year except 1989-90, when it fell to 50%. With the exception of 1989-90, these rates are similar to those reported by Richdale (1957) for his study populations on Otago Peninsula in 1937-38 to 1952-53. There was no significant difference between our estimates of annual survival and those from the earlier period, even when we included the 1989-90 estimate (Table 4).

Apparent survival rates may have been depressed by emigration. However, of 339 adult birds seen at Double Bay and Mid-section between 1982 and 1994, only 20 (5.9%) were recorded elsewhere when last seen, despite intensive monitoring of nearby sites in 1990-94 (Table 2). Emigration is therefore unlikely to have had much impact on apparent survival rates in any one year.

TABLE 4 LONG-TERM VARIATION IN ANNUAL ADULT SURVIVAL RATES ON OTAGO PENINSULA.

	n	PERCENT ANNUAL SURVIVAL		SD
		RANGE	MEAN	
1937-38 to 1952-53 (Richdale 1957 Table 72)	16	74-94	85.4	7.0
1981-82 to 1991-92 (This study)	10	49-100	83.2	13.2
This study excluding 1989-90	9	80-100	87.0	6.0

Mann-Whitney U test comparing 1937-38 to 1952-53 and 1982-83 to 1991-92: p = 0.38.

Survival and recruitment of pulli and juveniles

No statistical method was immediately available to adjust the recovery rates of banded pulli for varying effort and the declining opportunity for recovery towards the end of the study. We therefore report the raw return rates, realising that these are biased estimates of actual survival (Table 5). Data from the 1990-91 cohort are not included because there has been limited opportunity for recruitment. Preliminary indications are for poor recruitment. Of 13 birds released, only one (No. 11166) had appeared as an adult by 1993-94 (at Otanerito Bay, Banks Peninsula).

5.3 SEXING FROM MEASUREMENTS

A scatter plot of foot length vs head length for the calibration sample of known-sex birds showed reasonable separation of the sexes, although there was clearly some overlap (Fig. 2). The heads of males average 6 mm longer than females, and their feet average 5.5 mm longer (Table 7). These differences are statistically significant, as noted previously by Darby & Seddon (1990).

The major axis of the scatter plot (Fig. 2) had a slope of approximately 1.0, indicating that sexual variation in foot length was approximately equal to that in head length. There is therefore no basis for differential weighting of head and

TABLE 5 RETURN OF BANDED PULLI AS ADULTS (? 2 YEARS OLD) AT DOUBLE BAY AND MID-SECTION, OTAGO PENINSULA. SEPARATE COUNTS ARE GIVEN OF RETURNS TO THE NATAL AREA (DB+MS), AND OF TOTAL RETURNS TO ANY BREEDING AREA.

COHORT	NUMBER BANDED AND RELEASED	RETURNED TO DB+MS		TOTAL RETURNED	
		NUMBER	%	NUMBER	%
1981-82	61	11	18.0	17	27.9
1982-83	70	8	11.4	24	34.3
1983-84	93	18	19.4	31	33.3
1984-85	98	3	3.1	4	4.1
1985-86	93	1	1.1	1	1.1
1986-87	7[1]	0	0.0	1	14.3
1987-88	56	14	25.0	21	37.5
1988-89	64	11	17.2	20	31.3
1989-90	45[2]	0	0.0	3[3]	6.7
TOTAL	587	66	11.2	122	20.8

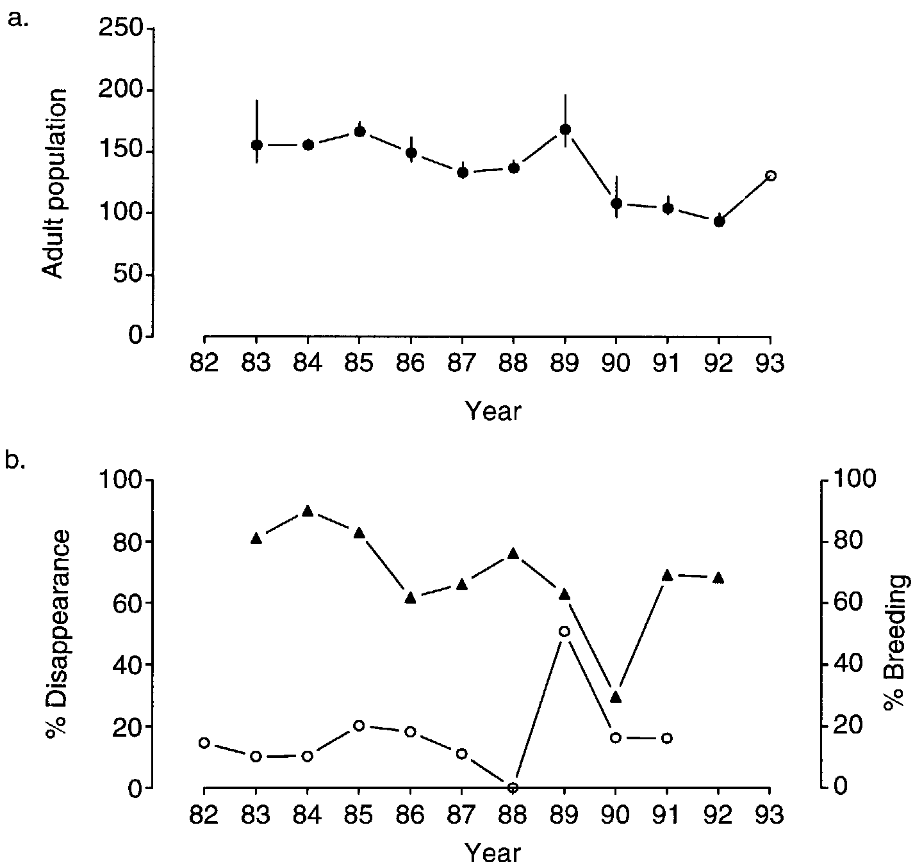
Notes:
Low tally partly due to egg removal at Double Bay (See Appendix 10.2).
Comprises 32 pulli fed in captivity and then released and 13 pulli not captive-fed. A further 6 banded captive-fed pulli released and recovered dead before 1 June are excluded from this analysis.
None of these 3 birds (10372, 10393, 10399) had been fed in captivity.

The earliest that a pullus can be sighted in adult plumage is 2 years after banding. Some birds are not seen for longer, either because they delay breeding (Richdale 1957) or because they are present but not sighted. The maximum lag recorded was of a bird fledged in 1983-84 but first seen as an adult in 1991-92 (Table 6).

TABLE 6 YEAR IN WHICH FIRST SEEN AS AN ADULT (<_ 2 YEARS OLD)

COHORT	83-84	84-85	85-86	86-87	87-88	88-89	89-90	90-91	91-92	92-93	93-94	TOTAL
1981-82	5	8	3	1	0	0	0	0	0	0	0	17
1982-83		15	6	1	1	1	0	0	0	0	0	24
1983-84			18	5	4	1	1	02	0	0	0	31
1984-85				1	0	2	0	1	0	0	0	4
1985-86					0	0	0	1	0	0	0	1
1986-87						1	0	0	0	0	0	1
1987-88							11	5	04	0	1	21
1988-89								11	7	2	0	20
1989-90									0	3	0	3
TOTAL	5	23	27	8	5	5	12	20	11	5	1	122

FIGURE 1



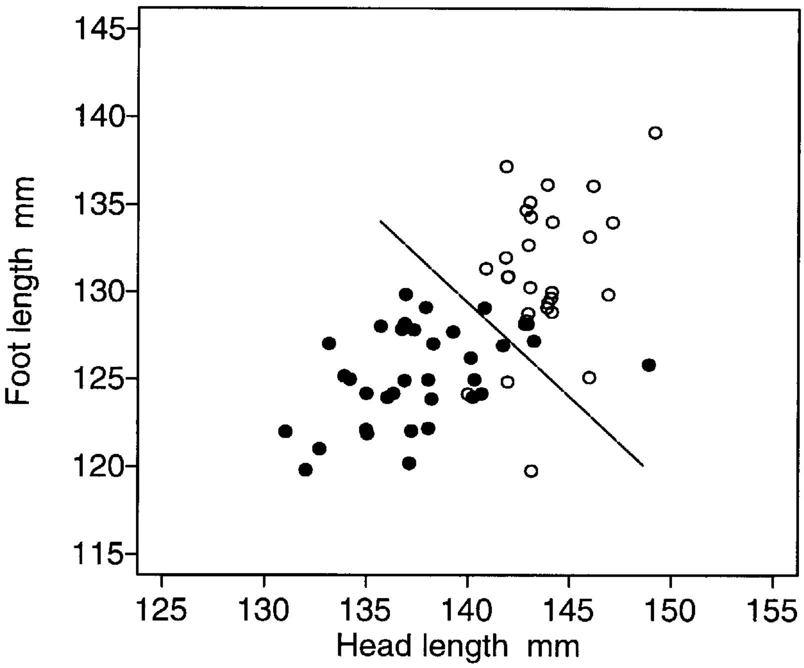
(a) Annual variation in the population of adult yellow-eyed penguins at Double Bay and Mid-section, Otago Peninsula. "Adult population" is Jolly-Seber estimate with 95% confidence limits calculated by the method of Manly (1984). No Jolly-Seber population estimate can be calculated for 1993-94; the open circle is based on the assumption that 10% of all adults were not sampled in 1993-94. Population estimates include non-breeding adults, but have an unknown bias due to the search method (see text).

(b) Annual variation in disappearance rate (circles) and proportion of adults breeding (triangles). "% disappearance" is the Jolly-Seber estimate for the period from the indicated breeding season to the following one. "% breeding" was calculated from twice the number of nests found divided by the Jolly-Seber population estimate.

TABLE 7 MEASUREMENTS OF KNOWN-SEX YELLOW-EYED PENGUINS

	n	RANGE	MEAN	SD
HEAD LENGTH (MM)				
MALES	29	140-149	143.7	1.95
FEMALES	34	131-149	137.6	3.59
FOOT LENGTH (MM)				
MALES	29	120-139	130.9	4.22
FEMALES	34	120-130	125.2	2.71
HEAD + FOOT (MM)				
MALES	29	263-288	274.6	5.23
FEMALES	34	252-275	262.8	5.32

FIGURE 2 RELATIONSHIP BETWEEN HEAD LENGTH AND FOOT LENGTH FOR KNOWN-SEX YELLOW-EYED PENGUINS FROM OTAGO PENINSULA (N=63). FEMALES MALES O. POINTS OFFSET SLIGHTLY TO REVEAL HIDDEN POINTS. DOTTED LINE INDICATES CRITERION USED FOR SEXING (HEAD LENGTH + FOOT LENGTH = 268.9 MM).



foot measurements when assigning sex, and the sum of the two measurements can be expected to work as well as a more elaborate discriminant function. We added head length and foot length to obtain a single index for sexing. The index was bimodal (Fig. 3), and the mean for males was 11.5 mm greater than that for females. As the standard deviations were approximately equal for males and females (Table 7), the average of the two means (268.9 mm) was chosen as a sexing criterion: birds with head+foot index of 269 mm or more were likely to be male, and smaller birds were likely to be female. This rule successfully classified 85.7% of the calibration sample (n = 63); six females and three males were misclassified by the criterion. Almost identical results were obtained for the test sample, which included juveniles (Table 8).

Applying the head+foot criterion to adults measured on Otago Peninsula since 1990-91, 124 birds were classified as females and 156 as males. The distribution of the index was only weakly bimodal and there was considerable overlap between the sexes (Fig. 4). Many of these birds were known to be paired to birds that were also measured, so that birds that were larger than their mate were likely to be males and vice versa. The size difference between mates had an essentially unimodal distribution (Fig.5; mean = 11.3 mm; SD=5.90 mm; n=258). However, some pairs comprised two birds of similar size (the index differed by less than 4 mm between the members of 30 pairs (11.6%).

The database recorded breeding attempts by 930 adult birds on Otago Peninsula up to and including the 1992-93 season. For 115 of these only one bird was identified, and their 'pairing network' was therefore of length 1. Pairing networks ranged in size from 1 (i.e. mate never identified) up to 17 birds, although most networks (56.2%, n=427) comprised only a pair.

FIGURE 3 SIZE INDEX (HEAD LENGTH + FOOT LENGTH) FOR KNOWN-SEX BIRDS FROM OTAGO PENINSULA (N=63). FEMALES SHADED. DOTTED LINE INDICATES 268.9 MM CRITERION USED FOR SEXING.

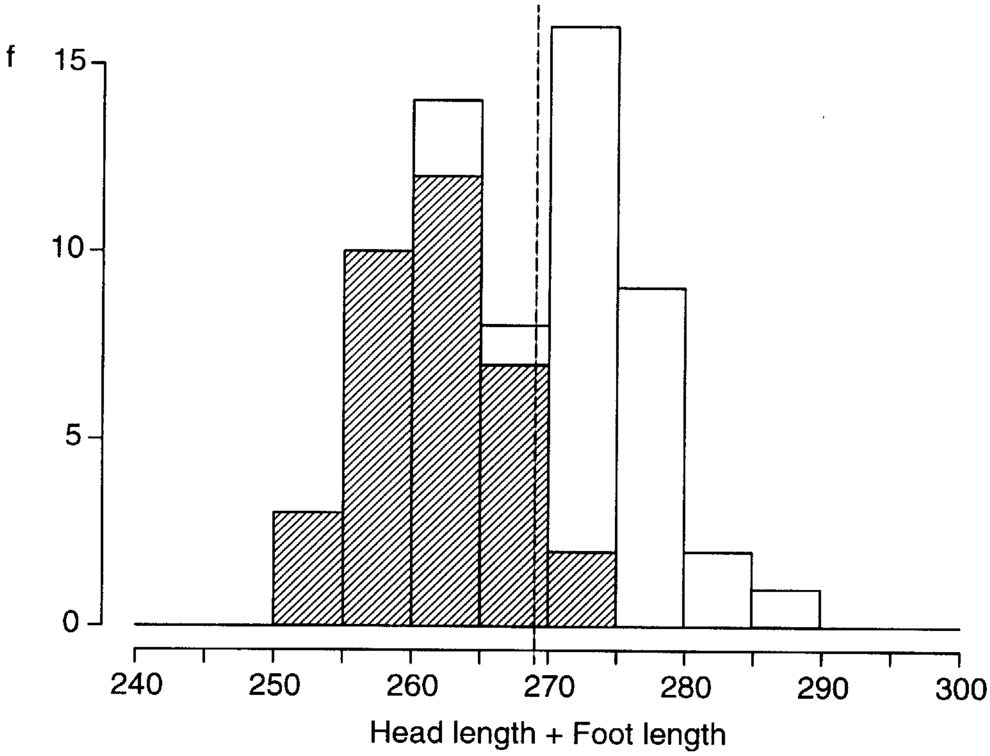


TABLE 8 SEX DETERMINED FROM MEASUREMENTS OF A TEST SAMPLE OF KNOWN-SEX BIRDS.

	CORRECTLY SEXED %	n
JUVENILE		
MALES	80.0	10
FEMALES	100.0	5
ADULT		
MALES	84.6	18
FEMALES	87.5	8
TOTAL	85.4	41

FIGURE 4 SIZE INDEX FOR BIRDS OF UNKNOWN SEX FROM OTAGO PENINSULA (N=280). DOTTED LINE INDICATES CRITERION USED FOR SEXING. INSET SHOWS INTERPRETATION OF HISTOGRAM AS THE SUM OF TWO NORMAL DISTRIBUTIONS FOR MALES AND FEMALES WITH MEAN AND SD AS IN TABLE 7.

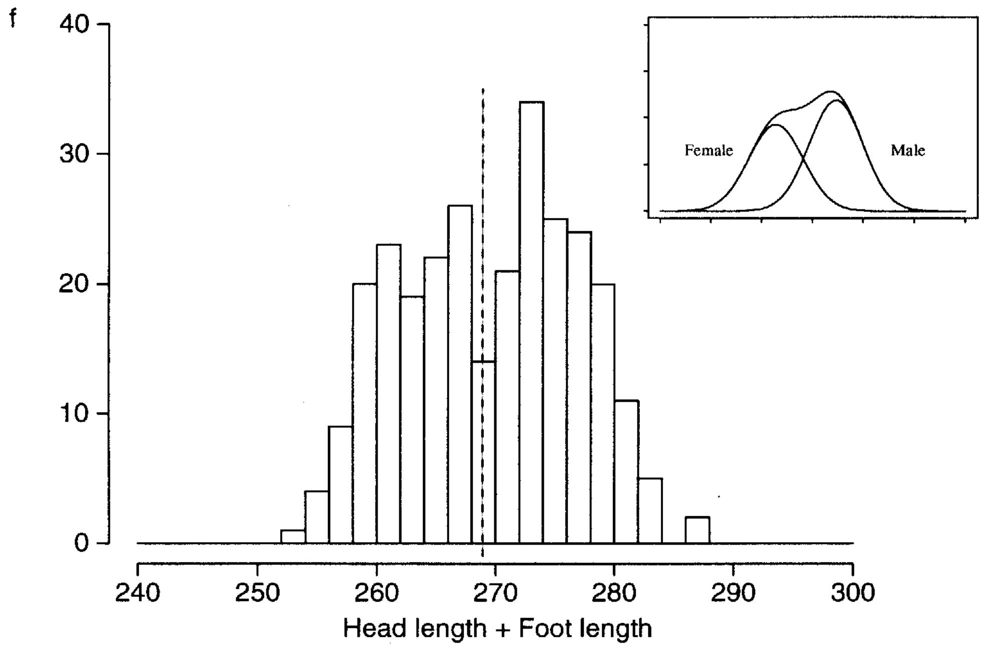
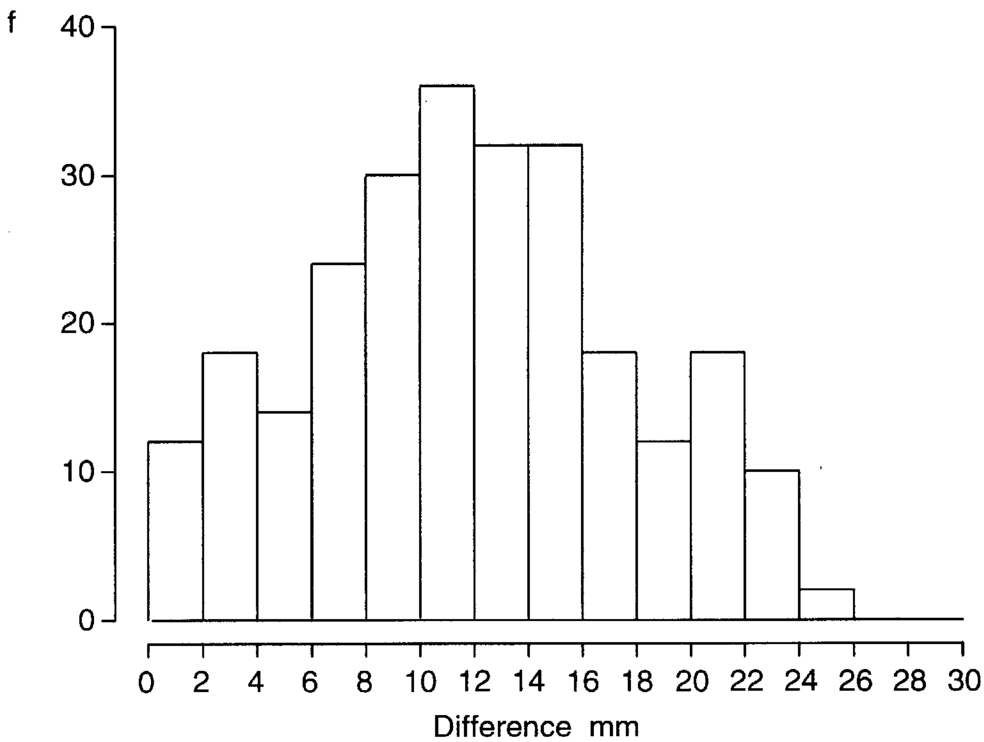


FIGURE 5 SIZE DIFFERENCE (HEAD LENGTH + FOOT LENGTH) BETWEEN MATED BIRDS FROM OTAGO PENINSULA (1990-91 TO 1993-94) (N=258 PAIRS).



6. Discussion

6.1 DATABASE ENTRY AND CHECKING

The banding database is substantially complete to date, requiring only minor adjustments as new information comes to hand. Historical nesting data have been entered only in a skeleton form because breeding data were outside the scope of the contract. Retrospective analysis of breeding success will require further checking and data entry.

The structure and operation of the database are discussed in a separate report (Efford et al. 1994, unpubl. Landcare Research contract report LC9495/38).

6.2 POPULATION ANALYSES

Mark-recapture methods

The mark-recapture analysis provided estimates of population size at Double Bay and Mid-Section that related to the entire adult population rather than just to those birds that actually bred in a particular year. Some assumptions of the method are unlikely to have been met, particularly the need for equal probability of sighting. Two sources of heterogeneity are apparent:

- Subadult and adult non-breeders form a separate stratum of the population that does not mix completely with established breeders. This results in incomplete mixing of the marked and unmarked fractions of the population.
- Breeders are more likely to be located if they were recorded the previous year because of the search procedure used.

The Jolly-Seber method is expected to underestimate actual population size in these circumstances, but the estimates are nevertheless more accurate than those from non-statistical methods (e.g., Nichols & Pollock 1983). Survival estimates are relatively robust to heterogeneity (e.g., Pollock et al. 1990). The problems of heterogeneity may probably be overcome with more elaborate mark-recapture models that allow for age structure and serial dependence of capture probability (e.g., Lebreton et al. 1992; Cormack, 1994).

Jolly-Seber estimates of survival are known to be subject to particular biases that may modify their pattern. As the errors of successive pairs of estimates are negatively correlated, the zero estimate of mortality in 1988-89 before the extreme 1989-90 event may be an artefact. Apparent mortality tends to increase towards the end of a study if the probability of sighting differs between birds (Carothers 1979). With data from more years the estimated survival of adults in 1990-91 and 1991-92 will probably increase slightly.

Band loss is a potentially serious source of bias in estimates of survival rate (Arnason & Mills 1981). We have made no formal assessment of band loss. The two known instances suggest the rate is low, but wear from a previous band is unlikely to be visible after the moult so the actual rate is likely to be much higher. C. Lalas (pers. comm.) has reported a high rate of band loss among fledglings on Green Island, where the rocky terrain probably causes unusual wear.

Annual survival and population change

Adult mortality was low (<_ 20%) in all years except 1989-90 when a mysterious episode of mortality occurred in December-February (Gill & Darby 1993). Numerous adult birds were found dead. Although they were slightly lighter than unaffected live birds, the difference was too small to suggest starvation as a cause of death, and no pathogens or toxins were isolated (Gill & Darby 1993). We estimate here that 50% of adults at Boulder Beach died during the 1989-90 breeding season or before the next season, about 3 times the long-term average.

The reduction in the annual number of adults seen between 1989-90 and 1990-91 (54%) was much greater than the estimated population decline (36%). This was due to a low probability of sighting in 1990-91 (53%). We believe this to be a reflection of the failure of many adult birds to breed in 1990-91 as search intensity remained high.

It is premature to say whether the adult population at Double Bay and Mid-Section has recovered from the 1989-90 crash. This must wait until Jolly-Seber population estimates are calculated for 1993-94 using recovery data from the 1994-95 breeding season.

Apart from the unusual mortality in 1989-90, there was little variation in adult survival from year to year. Van Heezik & Davis (1990) inferred that an adverse change in diet caused 15% of adults to starve during or just after the moult in 1985-86. Our estimate of adult mortality in this year (20%) was greater than that in 1984-85 (10%), but upward and downward fluctuations of this magnitude occurred frequently in Richdale's time and after 1985-86.

Survival and recruitment ofpulls and juveniles

About 21% of pulli banded at Boulder Beach (Double Bay and Mid-section) were recovered as adults, including 11% found as adults away from their natal areas. Other areas were not generally searched as intensively, so it is probable that many more were recruited elsewhere and not found. Actual mortality over the 2 years after fledging was therefore probably substantially less than 80%.

The survival of pulli varied dramatically between cohorts. Return rates were either greater than 27% or less than 7% for all cohorts except 1986-87, when only seven banded pulli were released. As a result, the age structure of the population can be expected to show a succession of strong and weak cohorts. Weak cohorts coincided with years of poor adult survival (1985-86, 1989-90), except for the 1984-85 cohort, which was 1 year old when adult survival was low in 1985-86.

Good recruitment from the 1988-89 cohort appears to be an anomaly: members of this cohort experienced as juveniles the conditions that led to the high adult mortality in 1989-90. The "catastrophe" of December 1989 - January 1990 appears particularly to have affected breeding adults. This in turn obviously had an impact on the survival of their chicks, most of which were taken into captivity for a period. However, it is not possible to separate the reduced viability of captive-reared chicks (most of those released in 1989-90) from stresses suffered by the same cohort as juveniles in 1990-91.

Proportion of non-breeding adults

Richdale (1957: Table 57 p.131) estimated that breeders formed 62% of the total population (adults + juveniles). Excluding juveniles for comparability with the mark-recapture estimates from our study, the proportion was 70.5%. If we double the number of nests to estimate the breeding population and divide by the Jolly-Seber N, the corresponding figure from our data was 68.8% averaged over 1983-1993. These proportions are remarkably similar. However, we dispute Richdale's (1957: 131) suggestion that the total population may be extrapolated from the number of nests in any one year. The proportion of adult-aged birds actually breeding in any year was extremely variable in our study (range 30% - 90%), and estimates based on this proportion would be correspondingly imprecise.

6.3 SEXING FROM MEASUREMENTS

Darby & Seddon (1990) reported that 27 adult males and 22 adult females had been sexed by dissection and measured. These records appear in the present study split between the "calibration" and "test" samples, with some additional data. The mean head and foot lengths reported here are within 1 mm of those previously reported (Darby & Seddon 1990, Table 2.1), and the overlap of male and female measurements was similar (14-15%).

When two birds are clearly paired as male and female, the measurements of the mate may be treated as additional data when sexing an individual. This effectively doubles the amount of information available on which to base determination of sex. Trials of such an extended morphometric technique should be undertaken when more data are available from known-sex pairs. If large birds do not select large mates, and vice versa, the proportion of breeding birds mis-sexed can be expected to decline to approximately 0.15 x 0.15, or approximately 2%, which would seem an acceptable level.

The main error in this technique is likely to arise from errors in the recognition of mated pairs. The minor mode near the origin in Fig. 5 may result from a small number of mistakes in determining mates (i.e., same-sex "pairs"). If, by chance, half of these individuals were misclassified, the overall error rate climbs to around 8%. We note that measurement of both members of a pair within one breeding season may require numerous nest visits. Reliance on body weight alone when comparing size between members of a pair is likely to be less satisfactory than linear measurements for the same reason that body weight alone is a poor indicator of the sex of individuals.

Retrospective analysis of pairing networks showed that some economies could be achieved by extrapolating to known mates, but these were not on the scale of those achieved by Richdale (1957). The present dataset arises from generally less intensive data collection over a much larger area, so many mates are unknown and pairing networks tended to be truncated. The episode of adult mortality in 1989-90 also cut short many developing pairing networks.

We look forward to the development of sexing methods for penguins based on DNA fingerprinting techniques (cf. Millar et al. 1992). Even if such tests are expensive, they may be more cost-effective for some studies than collecting behavioural data.

6.4 CONTINUATION OF BANDING STUDY

Knowledge from marked individuals is invaluable for interpreting extreme events such as the 1989-90 mortality. For this reason and others mentioned below there is a strong case for continuation of a centrally coordinated banding effort. Banding of young about to fledge is economical because breeding is synchronous and pulli may be captured with relative ease. Good recovery data are more expensive to obtain because juveniles disperse and not all adults are ashore at any one time, but without these the initial banding is useless. One possibility is that special attention is given to rigorous sampling of adult birds early in the breeding season at selected sites. It is probably not economical to attempt a complete census and the available effort may be better spent obtaining an approximately random sample (preferably exceeding 50% of adults) at a larger number of sites. Further analysis is needed for the design of an economical and effective monitoring system.

The mark-recapture analyses in this report assumed that unbanded birds were sampled (and banded) with the same probability that previously banded birds were recovered. This would not be true if some samples comprised sightings only, i.e., banded birds were recorded but unbanded birds passed by without being banded. Methods exist to incorporate "sighting only" samples in mark-recapture analyses (Lebreton et al. 1992), but such samples must be clearly distinguished.

We have demonstrated the use of banding data to estimate annual survival. Other benefits of banding include the recognition of dispersal movements, of which an obvious example is the high frequency of Otago-born birds among breeders on Banks Peninsula (e.g., Dilks & Grindell 1991 unpubl. DoC internal report). Movements between subpopulations are important in view of the likely genetic differences between them (Triggs & Darby 1989 unpubl. DoC internal report), and the possible importance of rescue effects for the survival of the mainland metapopulation.

7. Recommendations

Recommendations relating to the database are contained in a separate report (Efford et al. 1994 unpubl. Landcare Research contract report LC9495/38).

Mark-recapture methods that allow for age structure and serial dependence in sighting probabilities should be investigated for yellow-eyed penguins. Band loss should be measured on the South Island mainland by double banding or web-tagging a large sample of birds.

The unexplained 1989-90 mortality requires further investigation.

Detailed monitoring should be continued at Double Bay and Mid-section, Otago Peninsula. However, the demographic pattern described from there should be compared with the less complete records from other sites to establish how representative it is. Alternative monitoring schemes should be considered that would obtain rigorous samples of annual adult banding recoveries from a wider area.

The current system of forms should continue to be used.

The sexing method should be refined using a larger sample of known-sex adult birds when these become available. Sexing from DNA in blood samples should also be investigated.

8. Acknowledgements

We are grateful to the many field workers who contributed their efforts. Ruth Harper undertook much of the initial data entry. Peter Moore (DoC Science & Research) and Peter Dilks (DoC Canterbury Conservancy) supplied copies of banding returns for birds banded under their permits on Campbell Island and Auckland Island and on Banks Peninsula. Rod Cossee (National Banding Office) provided a computer file of recoveries reported to the Banding Office before 1992, and details of J-band usage.

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10. Appendices

10.1 SUMMARY OF YELLOW-EYED PENGUIN BANDING ACTIVITY 1973 - 1994

Yellow-eyed penguins have been banded by numerous field workers in the last 20 years. These efforts fall into six categories:

Intermittent banding in the 1970s by officers of the New Zealand Wildlife Service, Dept.Internal Affairs: Alan Wright (Otago Peninsula); Ross Marquand (Otago Peninsula); Dave Garrick (Catlins).

2. Banding by J. Darby and his assistants (particularly Adrian Patterson and Nick Spencer) mostly on Otago Peninsula, from 1981 to the present.
3. Banding by postgraduate students of the Zoology Department, Otago University during studies supervised by one or more of L. Davis, J. Darby, I. Jamieson, H. Moller. (Y.van Heezik; P.J. Seddon; K-A. Edge; H. Ratz).
4. Banding on expeditions to southern islands, mostly by staff of the N.Z. Wildlife Service or DoC (Table).

TABLE A1 BANDING OF YELLOW-EYED PENGUINS ON ISLAND EXPEDITIONS 1973-93

LOCALITY	OPERATOR	YEAR
CODFISH ISLAND	R. Nilsson	1975-76',1978-79, 1979-80'
	A. Wright	1979-80, 1980-81
	Y. van Heezik	1984-85
	P. Moore	1989-90
	D. Nelson	1992-93
ENDERBY ISLAND	J. Darby & P. Seddon	1985-86
CAMPBELL ISLAND	D. Garrick	1983-84
	P. Moore	1987-88,1989-90
	J. Amey	1991-92,1992-93

Fewer than ten birds banded

5. Banding by DoC Otago Conservancy and Science & Research staff associated with work on foraging behaviour (Moore et al. 1991 unpubl. DoC S&R internal report, pers. comm.; Green Island Lalas, 1992 unpubl. report to DoC).
6. Banding by Canterbury DoC staff on Banks Peninsula (Dilks & Grindell 1990 DoC S&R internal report, 1991; Dilks 1992 unpubl. report DoC Christchurch).

Almost all banding since 1980 has been under a National Banding Office permit held by John Darby. This has ensured relative uniformity of field procedures, some coordination of record keeping and consolidation of recovery data.

10.2 MANIPULATIONS OF STUDY POPULATIONS

The populations whose natural demography we set out to describe have been subjected to a variety of deliberate manipulations for the purposes of study and conservation management, in addition to disturbance over which we had no control:

Stomach pumping for diet analysis

Van Heezik (1988 unpubl. PhD thesis, 1990) and P. Moore (pers. comm.) collected stomach samples for diet analysis by water offloading. The technique is undoubtedly stressful, but no gross effects on survival or breeding performance have been documented. Between May 1984 and June 1986 van Heezik (1990: Table 1) sampled 512 adult yellow-eyed penguins from seven breeding areas on the Otago coast, particularly Nugget Point and the "Al" section at Boulder Beach, Otago Peninsula. Moore (pers. comm.) collected 185 samples from 85 individuals in the Boulder Beach "Al" section and at Long Point over the period February 1991 to July 1993.

Radio attachment

Moore et al. (1991 unpubl. DoC S&R internal report; pers. comm.) glued radio transmitters (weight 42 g) or time-depth recorders (weight 110 g) to the backs of selected adult birds in the Boulder Beach "Al" section and in the Catlins before and during the breeding season. The numbers of birds monitored in each year were as follows: 1990-91 (6 Al); 1991-92 (14 Al; 13 Catlins); 1992-93 (14 Al; 7 Catlins). Transmitters were removed from all but one bird after a maximum of 3 weeks; one bird disappeared in 1990-91 before its transmitter could be removed.

Egg removal

One egg was removed from each of 26 nests at Double Bay in late October 1986 (J. Darby unpubl. data). A single egg was removed from each of 42 nests on Otago Peninsula in 1990-91, leaving one egg in each; 14 of these eggs turned out to be infertile or to contain a dead embryo. (Darby & Patterson 1991 unpubl. DoC S&R internal report). These manipulations were intended to reduce the feeding effort required by the parents and hence increase the probability that they would survive to breed the following year.

Clutch manipulation

K-A. Edge moved fertile eggs from nests at Double Bay and Mid-section to Pipikaretu and Ryans Beach, Otago Peninsula in 1992-9_3 and 1993-94 as part of an experimental study to determine the productivity of l- and 2-chick broods, and the effects on adult survival (Darby & Edge 1993, 1994 unpubl. report to DoC).

Chick hand rearing

The large unexplained mortality of adults in 1989-90 (e.g., Darby & Paterson 1990 unpubl. report to DoC; Gill & Darby 1993) left many orphaned chicks, and others were removed to captivity with the intention of reducing the stress on their parents (see Egg removal). Surviving chicks were generally released at Moeraki regardless of their site of origin.

Predator trapping

Nest predators (cats (*Felis catus*), stoats (*Mustela erminea*), ferrets (*Mustela putorius*) and, incidentally, hedgehogs (*Erinaceus europeus*) and ship rats (*Rattus rattus*) have been kill-trapped before and during the breeding season in some years and at some sites (Darby & Seddon 1990; B.McKinlay pers. comm.).