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SURVIVAL AND MORTALITY IN A POPULATION OF ADÉLIE PENGUINS[1]

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Abstract. Life table and survivorship estimates were calculated for Adélie Penguins (*Pygoscelis adeliae*) of known age, sex, and breeding status. Fledglings had been banded and web-punched in nine consecutive breeding seasons at Cape Crozier, Ross Island. During four later seasons the returns of 2- to 14-yr-olds were recorded. Adjustments for band loss and emigration were made in the data. Survivorship estimates were also calculated for the Yellow-eyed Penguin (*Megadyptes antipodes*) using Richdale's (1949, 1957) data. Results indicate that breeding is risky, especially in the Adélie Penguin and particularly among younger breeders. In both species, females breed at younger ages than males and in any mature age class a greater proportion of females than males breed. These factors result in higher mortality among females and a sex ratio that changes to favor males in the older age groups. The oldest individuals tend to be those that are habitually inept breeders or non-breeders. The higher annual mortality and shorter life-span in the Adélie Penguin compared to the Yellow-eyed Penguin are probably due in part to heavier predation pressure.

Key words: Adélie Penguin; annual survivorship; Antarctica; life table; New Zealand; predation; sex ratios; Yellow-eyed Penguin.

INTRODUCTION

Among higher vertebrates penguins are relatively easy to census, capture, mark, and observe. Not surprisingly, one of the earliest avian population studies of a long-lived species was conducted on the Yellow-eyed Penguin (*Megadyptes antipodes*), by Richdale (1949, 1957) at the Otago Peninsula, New Zealand. In the present paper aspects of Adélie Penguin (*Pygoscelis adeliae*) population biology are presented and contrasted with the Yellow-eyed Penguin. Data for the latter species come entirely from Richdale's work, although life table calculations are our responsibility.

These two species are similar in that they breed annually, mated adults produce a maximum of two fledglings per breeding attempt, and they are similar in body size. They differ in that the Adélie seems to lead a more rigorous life. It is a highly migratory, diurnally active, open-nesting, and colonial penguin of high latitudes whereas the Yellow-eyed is a sedentary, nocturnally active (on land), burrow-nesting and noncolonial penguin of much lower, milder latitudes. Adélies raise their young during a 3-mo period but Yellow-eyed Penguins do so in 5.5 mo.

METHODS

The Adélie Penguin was studied at Cape Crozier, Ross Island, Antarctica (77°31′S, 169°23′E), site of a large breeding population (Fig. 1). Approximately 173 000 breeding adults were present in the Crozier West Rookery, and no detectable change in population size was noted during the period of this study (Oelke 1975, Butler and Müller-Schwarze 1977).

Each year from 1962 to 1970, Johns Hopkins University personnel banded 2000–5000 chicks just before fledging. Numbers on the aluminum wing bands were large enough to be read with 8 × 30 binoculars from a distance of 10 m. In 1964 the band design was improved; penguins having the old-style band, as described in Sladen and Penney (1960), were caught in a hand net and their band was exchanged for a new one, as described in Sladen and LeResche (1970). In subsequent years if any bands showed signs of opening, their owners were caught and the band was readjusted. In many cases this could be accomplished by placing one hand over a bird's eyes (to quiet it) while it incubated eggs and with the other hand adjusting or closing the band.

As a check against band loss, tiny holes were punched into the webs of a chick's feet using a leather punch. The number and location of punch holes (outer vs. inner web; right vs. left foot) were different for each year of banding. During November and January population peaks in the 1968–69, 1969–70, 1974–75, and 1975–76 austral summers, surveys were conducted to look for birds that had lost their bands. All colonies (groups of contiguous territories: Penney 1968) in study areas B, C, and part of N (Fig. 1) were circled

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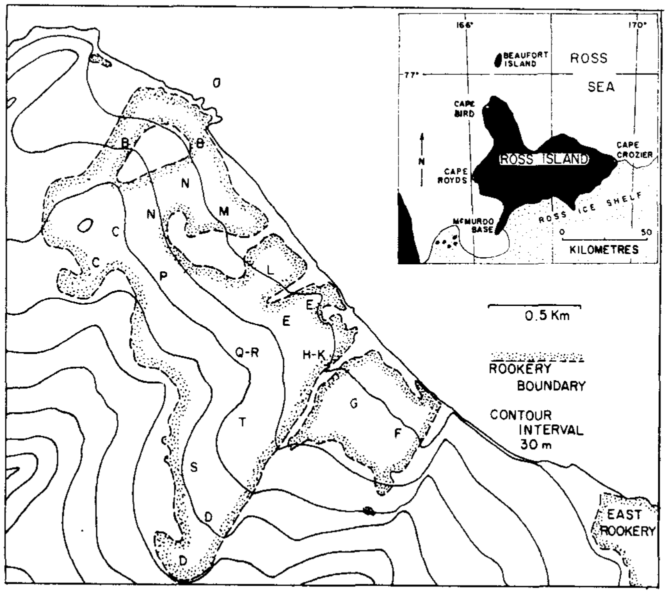

FIG. 1. The study areas designated by letters, set up by the United States Antarctic Research Program (USARP) Bird Banding Program at Crozier's West Rookery, and (insert) the location of Cape Crozier relative to other rookeries in the southern Ross Sea.

while the observer looked only at penguin feet. When a web-punched foot was sighted, the observer then looked to see if the bird was banded. If it had no band, it was caught and rebanded.

Only sightings of banded birds during the 1968–69, 1969–70, 1974–75, and 1975–76 field seasons were included in this analysis because surveys for banded penguins were known to be as complete as humanly possible during those seasons (Table 1). Furthermore, only birds banded in study areas B and C (two of four areas at Crozier where chicks were banded) were included in analyses because the western third of Crozier's West Rookery (where B and C are located) was most easily accessible and most intensively studied. Since Adélies tend to breed very near to their natal colonies (LeResche and Sladen 1970), it is most likely that if a bird from one of these two areas was not found it was not present. To be sure, the middle third of the rookery (includes banding area E) was searched almost as thoroughly, i.e., virtually every day. The eastern third of the West Rookery (includes banding area D) and the East Rookery were searched for banded birds each year during the occupation and reoccupation periods (cf. Sladen 1958) when seasonal peaks in the population occur. Data for birds 2–4 yr of age were gathered during the 1968–69 and 1969–70 seasons. Data for 5- to 14-yr-olds were gathered during the 1974–75 and 1975–76 seasons. Dates for data gathering at Cape Crozier were as follows: 24 October 1968–17 January 1969, 21 October 1969–5 February 1970, 19 October 1974–26 January 1975, and 20 October–17 December 1975.

RESULTS

Adjustments for band loss, emigration and comparability of years

The results of web-punch surveys to detect band loss are shown in Table 2, where the proportion of birds having lost bands in each cohort was compared to the age of the band in years. Because in some years a number of chicks was web-punched but not banded, we had to determine the percentage decrease in the proportion of birds having bands in subsequent years. Using the resultant fitted curve for band loss, recoveries as shown in Table 2 were adjusted in each age group by the formula:

$$z = \frac{x}{1 - y},$$

where x = number of bands recovered, y = proportion of bands lost, and z = number of bands recovered if there had been no loss. Recoveries adjusted for band loss are summarized in Table 3. For cohorts originally banded with the old-style band, recoveries in later years were adjusted using the formula shown in the footnote of Table 3. We had to assume that band loss for both band styles was equal, although it is likely that loss was slightly higher for the old style; we also assumed that all birds were rebanded at age 3 yr. A

TABLE 1. Band recovery data from 1968–69, 1969–70, 1974–75, and 1975–76.

Year banded	Number banded	Age of recovery (yr) 2	3	4	5	6	7	8	9	10	11	12	13	14
1961–62	2308						34	27					5	4
1962–63	4110					104	95					31	22	
1963–64	4998				216	172					73	41		
1964–65	3080			264	181					83	34			
1965–66	3800		320	258					72	40				
1966–67	3600	355	279					113	71					
1967–68	4000	428					301	192						
1968–69	2950					363	216							
1969–70	2322				301	197								

small proportion was in fact rebanded at ages 2, 4, and 5 yr.

Besides band loss, emigration can also result in the apparent disappearance of a bird from a population. Fortunately, two of the four other Adélie rookeries (Penney 1968) in the southern Ross Sea were visited by ornithologists searching for banded birds for extended periods almost yearly through 1971, and the other two were visited intermittently. Thus we have approximate emigration rates for this population. Fig. 2 compares the number of banded Crozier birds at four other rookeries and relates these numbers to the distance from the Cape Crozier West Rookery. These other rookeries and their distances were: Crozier East Rookery, 2 km; Cape Bird and Beaufort Island, each 61 km; and Cape Royds, 100 km (Fig. 1). Only birds 5 yr of age and older, through 1971, were used in Fig. 2 because many younger birds characteristically wander from rookery to rookery but then eventually return to their natal rookeries for breeding. Given that appreciable movement was detected in only 51 birds out of 18 296 banded (0.28%, $\sigma < 0.01$), emigration does not appear to be a major factor in the Crozier population. Even so, the emigrants were included in Table 1 and in further analyses.

Two sets of years were used in order that as many age groups as possible were represented in analyses, 1968–69 to 1969–70 for 2- to 4-yr-olds and 1974–75 to 1975–76 for 5- to 14-yr-olds. Mortality during the two sets of seasons did, however, appear to differ slightly as shown by comparing three age groups, 5-, 6-, and 7-yr-olds, that occurred in both sets of years (Table 4). Lumped survivorship of these ages was 83% (σ = 0.04) from 1968–69 to 1969–70 and 63% (σ = 0.02) from 1974–75 to 1975–76 (Table 4). The difference is statistically significant (adjusted $\chi^2 = 32.02$, $P < .01$, df = 1; Steel and Torrie 1960: 371). It is possible that the 63% survivorship is a conservative estimate. Some

TABLE 2. Estimation of band loss as a function of band age. Based on surveys conducted in 1968–69, 1969–70, 1974–75, and 1975–76.

Band age (yr)	Birds inspected (n)	Proportion currently banded	Proportion originally banded and web-punched*	Observed band loss (%)	Fitted band loss† (%)
2	15	1.00	1.00	0.0	1.0
3	45	0.97	0.99	2.0	1.3
4	31	0.87	0.89	2.0	1.7
5	51	1.00	1.00	0.0	2.2
6	89	0.99	1.00	1.0	2.9
7	66	1.00	1.00	0.0	3.8
8	16	1.00	1.00	0.0	4.9
9	13	0.92	0.99	7.1	6.4
10	23	0.74	0.84	11.9	8.4
11	…	…	…	…	11.1

* Some birds were only web-punched in some years.
† Curve fitted to exponential equation: $y = 0.574e^{0.269x}$, where y = band loss and x = age of band in years.

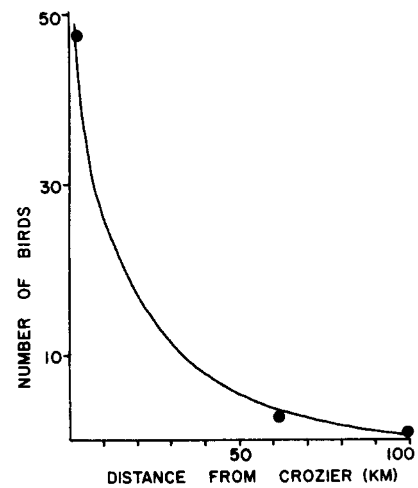

FIG. 2. The number of 5-yr or older Adélies banded at the Cape Crozier West Rookery and subsequently sighted at other rookeries in the southern Ross Sea compared to the distances between these and Crozier's West Rookery; data were combined for Cape Bird and Beaufort Island because they were equidistant from Crozier. The curve is described by the equation, $y = 44.4e^{-0.039x}$.

TABLE 3. Band recovery data adjusted for band loss. Recovery data from Table 1; correction data from Table 2.

Year banded	Number banded	Age of recovery (yr) 2	3	4	5	6	7	8	9	10	11	12	13	14
1961–62	2308						35*	28*					6*	5*
1962–63	4110					107*	98*					34*	24*	
1963–64	4998				221*	177*					78*	44*		
1964–65	3080			269	185					91	38			
1965–66	3800		324	262					77	44				
1966–67	3600	359	283					119	76					
1967–68	4000	432					313	202						
1968–69	2950					374	225							
1969–70	2322				308	203								

* All birds originally banded before the 1964–65 season were rebanded as 3-yr-olds. Therefore, band loss was adjusted for with the equation: estimated band loss (%) = $1.3 + 0.574e^{0.269(x-3)}$, where x = age of the bird or band in years (see Table 2, second footnote).

additional 5-yr-olds, and perhaps 6-yr-olds, but not older individuals may have arrived after our departure in mid-December 1975. This is because younger Adélie Penguins tend to arrive later at the rookery than older ones (LeResche 1971, Ainley 1975). On the other hand, there may have been real differences in mortality related to environmental conditions. Ainley and LeResche (1973) showed that pack ice conditions could have major effects on the breeding biology and productivity of Adélies. Environmental conditions might also have affected mortality enough that there would be notable differences between years, as observed for Yellow-eyed Penguins by Richdale (1957). For instance, the unusually heavy and persistent pack ice in the 1968–69 season delayed Adélie migration to Crozier and led to a low proportion of breeding birds (Ainley and LeResche 1973). Since mortality is so high in breeders (see below), being prevented from breeding might have resulted in increased survival of birds to the 1969–70 season. Additional census seasons may have allowed us to correct for this. In any case, it should be noted that the annual survivorship for 1974–75 to 1975–76 may be slightly low or for 1968–69 to 1969–70 slightly high, one group relative to the other.

Life table and survivorship estimates

Partial horizontal life tables were constructed (Tables 5, 6, and 7) using the data in Table 3. These are only partial life table analyses because data on age-specific fecundity are yet to be analyzed; it will be some time before they are available. Curves generated from the resultant survivorships are all monotonic as expected. The difference in survivorship (l_x) between the two sets of years is quite evident ($\chi^2 = 777$, $P < .05$, df = 3).

This difference suggests that the mortality of chicks or yearling birds was greater between 1961–62 and 1964–65 than it was between 1966–67 and 1969–70. It is interesting that annual survivorship values (Table 4) for these two sets of data are opposite in pattern to the l_x values. The fact that when l_x estimates are relatively low, annual survivorship estimates are relatively high, may reflect some sort of compensatory mortality. Another possibility is that band loss was greater during the first 3 yr of study when the old-style band was employed. Our correction factor, based on loss rates of the new-style band (Table 3, footnote), was perhaps not fully adequate. More information is needed to assess these premises.

The data on 5- to 14-yr-olds in Table 7 were used to generate a survivorship curve for Adélies (Fig. 3). When the same curve was extended to younger ages, data points diverged radically from it, due to the fact that many Adélies 4 yr of age and younger, and occasionally 5-yr-olds, had not yet returned to the rookery since fledging; by 6 yr, all Adélies that are going to return to their natal rookery have done so for the first time. Because of this it was not possible to generate survivorship curves for younger birds. Also presented in Fig. 3 is a survivorship curve for Yellow-eyed Penguins based on Ricklefs' (1973) survivorship

TABLE 4. Comparison of annual survivorship from year 1968–69 to 1969–70 with that from 1974–75 to 1975–76.

Age, year i	1968–69 to 1969–70: Number, year i	Number, year $i+1$	Annual survival	1974–75 to 1975–76: Number, year i	Number, year $i+1$	Annual survival
2	359	283	0.788			
3	324	262	0.809			
4	269	185	0.688			
5	221	177	0.801	308	203	0.659
6	107	98	0.916	374	224	0.599
7	35	28	0.800	313	202	0.645
8				119	76	0.639
9				77	44	0.571
10				91	38	0.418
11				78	44	0.564
12				34	24	0.706
13				6	5	0.833
T	1315	1033	0.786	1400	860	0.614

TABLE 5. Comparison of l_x values from 1968–69 to 1969–70 data with data from 1974–75 to 1975–76.

	1968–69 and 1969–70			1974–75 and 1975–76			
Age x	Number banded as chicks	Number recovered at age x	l_x	Number banded as chicks	Number recovered at age x	l_x	Ratio of increase
5	8078	406	0.050	2322	308	0.133	1.66
6	9108	284	0.031	5272	577	0.109	2.51
7	6418	133	0.021	6950	538	0.077	2.67
8	2308	28	0.012	7600	321	0.042	2.50

analysis of Richdale's (1957) data. We corrected Ricklefs' values to allow for the fact that the population increased by 230% during the study (Table 8). Richdale, in fact, attributed the increase to enhanced survival of adults. Comparison of survivorship curves indicated that Yellow-eyed Penguins live longer than Adélies. Only 0.2% of banded Adélies survived 14 yr. The oldest was estimated to be 16 yr. That bird was banded as an adult of unknown age but its behavior suggested that it was 4 or, perhaps, 5 yr old when banded. It would appear from the curve that 16 yr would be near the maximum age for Adélie Penguins. Richdale (1957) had known-age individuals of 17 yr, and some unknown individuals estimated to be ≈19 yr. The curve confirms his suggestion that the oldest Yellow-eyed would live for ≈22 yr or perhaps slightly longer.

The lumped annual survivorship of 1400 Adélies 5–13 yr old from 1974–75 to 1975–76 was 61.4% (σ = 0.01) based on the values presented in Table 4. Average annual survivorship based on the curve (survivors/100 birds originally banded) was 69.6% (σ = 0.17), which is fairly close to the other estimate. The lumped annual survivorship of 630 Yellow-eyed Penguins 5–13 yr old was 86.2% (σ = 0.02), as calculated from Richdale (1957: Table 69). Average annual survivorship based on the curve for the same Yellow-eyed Penguin age classes as calculated by Ricklefs but corrected for an increasing population (Table 8), was 87.2% (σ = 0.02). Annual survivorship is much lower in adult Adélies than in adult Yellow-eyed Penguins.

Factors affecting survivorship

It was possible to determine whether survivorship was related to age. The lumped annual survivorship of 61.4% was multiplied by the (corrected) number of birds observed in each age group during 1974 (column 5 of Table 4) to derive expected values. These were compared in a χ^2 test with those observed alive in 1975. For birds 6–13 yr old, annual survival was independent of age ($\chi^2 = 6.58$, $P > .05$, df = 6). This, however, was not true when breeding status and younger birds were considered (see below).

When Adélies were grouped by age, sex, and breeding status, interesting differences in annual mortality became obvious. To establish a sufficient sample among older individuals, birds 11 yr and older were combined into one group (Table 9). From these mor-

TABLE 6. Partial horizontal life table for the Adélie Penguin. Data from Table 3.

	l_x Year banded as chick								
Age (yr)	1961–62	1962–63	1963–64	1964–65	1965–66	1966–67	1967–68	1968–69	1969–70
0									
1									
2						0.100	0.108		
3					0.085	0.079			
4				0.087	0.069				
5			0.044	0.060					0.133
6		0.026	0.035					0.123	0.087
7	0.015	0.024					0.078	0.076	
8	0.012					0.033	0.051		
9					0.020	0.021			
10				0.030	0.012				
11			0.016	0.012					
12		0.008	0.009						
13	0.003	0.006							
14	0.002								

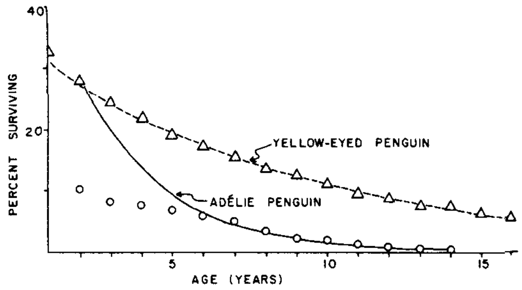

FIG. 3. A comparison of survivorship curves for Yellow-eyed Penguins at Otago Peninsula, New Zealand, during 1934–1952 and for Adélie Penguins at Cape Crozier during 1962–1976. The data points, for ages 5 yr and older, from Tables 7 and 8, were used to generate the curves, fitted by least squares.

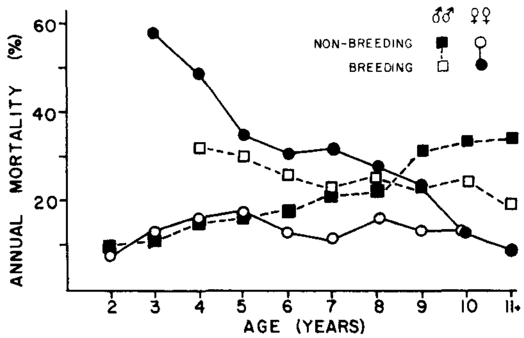

FIG. 4. Annual mortality of Adélies grouped by age, sex, and breeding status. The three-point moving averages are based on data in Table 9.

talities, three-point moving averages were calculated and are presented in Fig. 4. Mortality among breeding females declined from almost 75% in 3-yr-olds to 10% in those 11 yr and older (Table 9; $r = -.9653$, $P < .05$). Among nonbreeding females, mortality remained ≈12% ($r = .2538$, $P > .05$) throughout the age classes (female Adélies first breed at 3 yr; LeResche 1971). Mortality among breeding males also declined with age, from 36% in 4-yr-olds (the age of first breeding among male Adélies) to 18% in birds 11 yr and older ($r = -.8959$, $P < .05$), a change similar to that in females ($t = .050$, $P > .05$; test for homogeneity of regression, Steel and Torrie 1960:173). Among nonbreeding males, mortality increased from 7% in 2-yr-olds to 33% in birds 11 yr and older ($r = .8914$, $P < .05$).

Differences in annual mortality for birds of different age, sex, and breeding status relate to or affect the composition of Adélie populations in several ways. Among these, breeding status seems to be the most important controlling factor as the following analyses show, the data for which are presented in Table 9. The difference in annual survivorship between 1134 breeders (60.5%) and 697 nonbreeders (78.2%) regardless of sex, was highly significant (adjusted $\chi^2 = 37.8$, $P < .001$, df = 1). Age has a secondary effect on the mortality of breeders in that survival is very low in young breeders. Among 3- and 4-yr-old breeders ($n = 53$) annual survivorship was only 54.7% ($\sigma = 0.47$) compared to 72.5% ($\sigma = 0.02$) for breeders ($n = 1081$) 5–11+ yr of age (adjusted $\chi^2 = 8.79$, $P < .05$, df = 1). Age 5 yr was critical because there was no stiatistical difference when 3- to 5-yr-olds were compared with birds 6 yr of age and older. Mortality thus was high among breeders and especially high among the youngest two age classes. This is shown graphically in Fig.

TABLE 7. Partial horizontal life table for the Adélie Penguin. Data from Table 3 are averaged over both years of recovery.

Age (yr)	Number banded as chicks	Number recovered at age x	l_x
0	...	...	1.00
1	...	...	...
2	7 600	791	0.104
3	7 400	607	0.082
4	6 880	531	0.077
5	10 400	714	0.069
6	14 380	861	0.060
7	13 368	670	0.050
8	9 908	349	0.035
9	7 400	153	0.021
10	6 880	135	0.020
11	8 078	116	0.014
12	9 108	78	0.009
13	6 418	30	0.005
14	2 308	5	0.002

TABLE 8. Life table l_x values calculated by Ricklefs (1973) using Richdale's (1957) Yellow-eyed Penguin data, and corrected by the method of Payne (1977) for the fact that the population increased 230% during the study.

x (age in yr)	l_x*	"l_x"†
0	1.000	1.000
1	0.305	0.324
2	0.247	0.278
3	0.203	0.242
4	0.171	0.217
5	0.144	0.193
6	0.121	0.172
7	0.102	0.154
8	0.086	0.138
9	0.072	0.122
10	0.061	0.110
11	0.051	0.098
12	0.043	0.087
13	0.035	0.075
14	0.031	0.071
15	0.026	0.063
16	0.022	0.057

* l_x values from Ricklefs (1973: Table 4).
† "l_x" = $(l_x)(e^{rx})$, where $r = .059$.

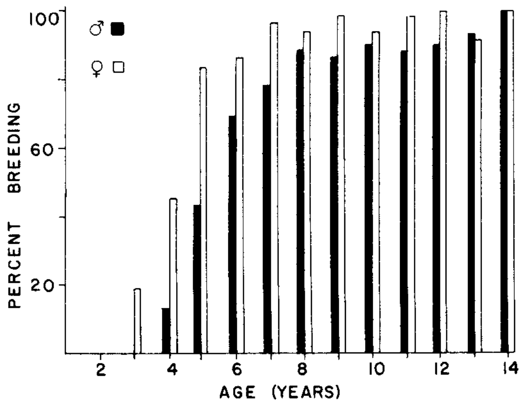

FIG. 5. The proportion of breeding individuals among male and female Adélies at each age.

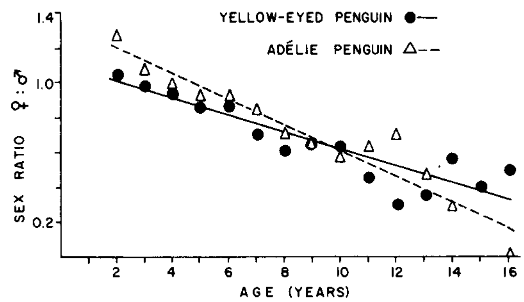

FIG. 6. The change in sex ratio with age within populations of Adélie and Yellow-eyed Penguins ($r = -.9532$ and $-.9056$, respectively).

4 where it also appears that for nonbreeders mortality increased only, if at all, among older individuals. A comparison of mortality between 10 yr and older nonbreeders (37.5%; $\sigma = 2.93$, $n = 8$) and younger nonbreeders (14.7%; $\sigma = 0.02$, $n = 633$) was not statistically significant (adjusted $\chi^2 = 1.63$), perhaps because the sample of older birds was not large enough.

The high mortality among breeders, especially young ones, the fact that females begin to breed earlier than males (average age of first reproduction for females, 4.70 ± 0.73, and for males, 6.80 ± 0.73; see DeMaster 1978), and the fact that a large proportion of older Adélie females (compared to males) breed (Fig. 5), led to higher mortality in females. This in turn led to a sex ratio that favored males more and more with greater age (Fig. 6) and accounted for the fact that the oldest Adélies were predominantly males. In fact, only 4 of 54 birds 10 yr or older were females (one 14-yr-old was a female). The sex ratio in Yellow-eyed Penguins changed in a similar but more gradual way ($t = 2.1392$, $P < .05$; test for homogeneity of regression, Steel and Torrie 1960:173); males predominated among the older birds but not to the same degree as in Adélie Penguins.

In light of these patterns, it is not surprising that the oldest Adélies shared the following characteristics: they tended to be males, they first bred at a late age, were nonbreeders during many of their years, and if they did attempt breeding were relatively unsuccessful (Ainley 1978; D. Ainley, R. LeResche, and W. Sladen, *personal observation*). Richdale (1957) did not provide information on whether a similar trend was true for *M antipodes*.

DISCUSSION

Annual survival among adult Adélies was much lower than in Yellow-eyed Penguins, particularly among younger birds. Part of the difference was due to the Yellow-eyed Penguin population increase during Richdale's (1957) study whereas the Adélie Penguin population studied here was stable. The remainder of the difference was probably related in some way to the different lifestyles and environments of the two species. It may be that the harsher conditions during winter and the longer distances they traveled during both migration and feeding during the summer, led to a higher mortality among Adélies. The latter were also subject to a higher rate of predation (see below). The higher mortality among Adélie Penguins should have been compensated for by higher reproductive success. The data for comparison between the two species are not yet ready for analysis.

It appears that activities associated with reproduction are very costly for Adélie Penguins in terms of energy; in reproducing they increase their mortality substantially, especially the younger birds. Breeding in this species, as it must be in many other long-lived species, is an adjustment between not breeding at too young an age but breeding soon enough to insure reproduction. By breeding, a bird greatly increases the risks of an early death.

These compromises, as well as other factors, such as younger birds being less efficient at feeding (see Ainley and Schlatter 1972), must be related to the fact that Adélies do not become reproductively mature until at least 3 or 4 yr old (Ainley 1975). The majority, in fact, do not first breed until 4–6 yr and the proportion of birds breeding increases gradually with age, reaching 94% of birds 12 yr and older (Ainley 1978; Fig. 7). In contrast, the youngest Yellow-eyed Penguin breeders are 2 yr old and the proportion of adults breeding reaches its maximum as early as 4 yr. The proportion of breeders among birds at least 12 yr is significantly higher in Adélies (94%; $\sigma = 0.1$, $n = 92$) than in Yellow-eyed Penguins (81%; $\sigma = 0.1$, $n = 177$; $t = 3.365$, $P < .01$; test for percentages, Sokal and Rohlf 1969:608). The earlier age of youngest breeders and the much greater proportion of younger birds (3- to 5-yr-olds) breeding, indicates indirectly that breeding at a young age is not as costly for Yellow-eyed Penguins. The Yellow-eyed Penguin sex ratio, which changes in a way similar to, but more gradual than that of Adélie Penguins, may suggest that mortality factors operate in the same way for the two species but at greater intensity for Adélies. This, plus the smaller proportion of birds 7 yr of age and older breeding in a given year, may account for the greater annual survival and longevity in Yellow-eyed Penguins.

Predation seems related closely to the high risk of breeding among Adélie Penguins. Predation by leopard seals (*Hydrurga leptonyx*) is well documented for Adélie Penguins (Penney and Lowry 1967, Müller-Schwarze and Müller-Schwarze 1975). These authors estimated that seals eat at least 1.4–5.0% of adults during the latter's breeding season each year. Based on a recent and more reliable but lower population estimate (Butler and Müller-Schwarze 1977), Adélie mortality due to predation within sight of the rookery is calculated at 2.3–7.3% of the adult population. Predation of Yellow-eyed Penguins by sea lions (*Neophoca hookeri*) also occurs (Spellerberg 1975, D. Ainley, *personal observation*) but has been reported very infrequently.

Leopard seals catch Adélies by waiting at the water's edge near the rookery. Several seals at Crozier are usually evenly spaced linearly along the beach. They also catch penguins in the ice pack during the summer but as far as we know this has been observed only once (D. Ainley, *personal observation*). Comparing the number of times breeding and nonbreeding Adélies must cross the line of leopard seals suggests one reason why breeding is so risky. To successfully rear young in an austral summer, breeders must pass through the seals an average of 47 times (data from Taylor 1962) but nonbreeders must pass through only four times (Ainley 1978). Since most of the trips occur in order to catch food for chicks, if the breeders lose their eggs or chicks early they are no longer "forced" to cope with the seals. Furthermore, nonbreeders (or unsuccessful breeders) are probably in better physical shape than breeders because during the few times that they leave the rookery, they are not pressured to feed and return quickly in order to relieve a mate or to tend chicks. If it is true that young breeders are less efficient at obtaining food, as suggested by Ainley and Schlatter (1972), then they may be less physically and energetically fit than older breeders. They may therefore fare even more poorly in coping with leopard seals. Because mortality is so high among the youngest Adélie breeders, 75% among 3-yr-olds and 40% among 4-yr-olds, one questions why Adélies risk breeding when so young, particularly at age 3 yr. The answer may be that birds breeding at 3 yr that survive tend to be highly productive breeders in subsequent years (D.

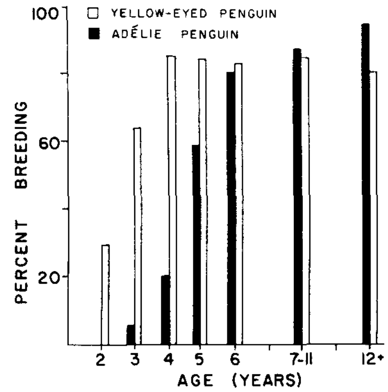

FIG. 7. The proportion of breeding individuals among Adélie and Yellow-eyed Penguins at each age. Some of the older age groups were combined to increase the samples. Data for Yellow-eyed Penguins are from Richdale (1949: Table 25).

TABLE 9. Annual survivorship among Adélies of known age, sex, and breeding status.

	Breeders				Nonbreeders			
Age (yr)	Number ♂♂	Percent disappearing ±SD	Number ♀♀	Percent disappearing ±SD	Number ♂♂	Percent disappearing ±SD	Number ♀♀	Percent disappearing ±SD
2					112*	7 ± 2		
3			8	75 ± 15	78	13 ± 4	67	10 ± 4
4	11	36 ± 14	34	41 ± 8	79	14 ± 4	43	21 ± 6
5	113	27 ± 4	150	30 ± 4	117	17 ± 3	37	16 ± 6
6	152	27 ± 4	164	35 ± 4	62	18 ± 5	29	14 ± 6
7	145	25 ± 4	148	28 ± 4	32	19 ± 7	10	10 ± 9
8	38	18 ± 2	30	33 ± 9	8	25 ± 15	3	0 ± 0
9	22	32 ± 10	18	22 ± 10	7	0 ± 0	5	40 ± 22
10	28	21 ± 8	19	16 ± 8	3	67 ± 27	2	0 ± 0
11+	34	18 ± 7	20	10 ± 7	3	33 ± 27		
T	543		591		501		196	

* This number includes both males and females combined, as few were sexed.

Ainley, R. LeResche, and W. Sladen, *personal observation*). This then is the opposite extreme from those birds that by not breeding or by habitually breeding unsuccessfully reach a rather old age.

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