

SURVIVAL ANALYSIS OF EGGS AND CHICKS OF ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*)

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ABSTRACT.—Survival analysis was used to examine the fates of eggs in six colonies of Adélie Penguins (*Pygoscelis adeliae*) at Cape Bird, Antarctica. Hatching success was 56.2% and fledging success for chicks was 63.3%, giving an overall reproductive success of 35.6%. The major cause of losses of both eggs and chicks was predation by South Polar Skuas (*Catharacta maccormicki*). The second-most important causes of egg and chick mortality were desertion and starvation, respectively, both of which resulted from inadequate timing of nest relief. Eggs were at risk of predation by skuas throughout the incubation period, while chicks were at risk for the first 30 days after hatching. The likelihood of desertion increased after the eggs had been incubated for 16 days and reached a peak at 22–24 days. Starvation occurred during the guard stage and was most likely to occur when chicks were 6–8 days old. Timing of breeding and clutch size were factors that influenced the survival of eggs through the initial stage of incubation. Nest location had a significant effect on the survival of eggs and chicks, from laying through the end of the guard stage. Eggs laid in 2-egg clutches and in central nests were most likely to produce chicks that fledged. Received 17 April 1985, accepted 22 November 1985.

ALTHOUGH the breeding biology of Adélie Penguins (*Pygoscelis adeliae*) has been studied comprehensively (Levick 1914, Sladen 1958, Sapin-Jaloustre 1960, Taylor 1962, Penney 1968, Spurr 1975), causes of breeding failure and the factors that influence these causes remain poorly understood. This is true of many colonial seabirds, and is due mainly to the complexity with which many factors affect reproductive success (Pugesek and Diem 1983).

Many workers have provided gross estimates of breeding success for *P. adeliae*, but only Taylor (1962) and Spurr (1975) quantified the causes for egg and chick losses. In even the most detailed of these studies, causes of mortality and the ages at which it occurred were monitored only at 10-day intervals for eggs and 5-day intervals for chicks (Spurr 1975). As a result, fully 59% of egg losses and 20% of chick losses were due to unknown causes.

Survival can be expressed as an age-specific mortality rate, or hazard function (q_x), which is computed from the proportion of a cohort surviving to each age interval, the survival curve (l_x). In practice, most ecological life tables are obtained by estimating the survival curve from a sampling of a population's age structure at

one time and under one set of environmental conditions (Collier et al. 1973). Using the age structure as a basis for survival curves is valid, however, only if the number of young born each year is constant (i.e. the size of all cohorts at birth is equal), a condition rarely met in natural populations (Ricklefs 1979). This problem can be addressed by following the survival of a single cohort through time, producing a "dynamic life table" (Southwood 1966). There are few examples of such tables (Collier et al. 1973), and those that exist have come mainly from long-term studies of marked populations of individually identifiable, known-age individuals (e.g. Ainley and DeMaster 1980, Halvorson and Engeman 1983). But even with these studies, the estimates of survival were hampered by losses from unknown causes and unknown ages at death (Collier et al. 1973). Consequently, corrections must be made for losses due to dispersal, for band (identification) losses, and, if data are grouped for more than one cohort, for changes in survival rates for each age class from year to year (Ainley and DeMaster 1980).

By contrast, in the medical sciences, where patients are closely monitored so that causes of death and time from a starting event (usually diagnosis of a disease, or surgery) to death are known, statistical techniques have been developed for analyzing survival (Cutler and Ederer 1958, Kaplan and Meier 1958, Gehan 1975, Gross

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and Clark 1975). A major advantage of these techniques is that they can be used to compare survival curves, either from different samples of the population under the same environmental conditions or from the same population under different environmental conditions.

Here we report on the survival of a large sample of eggs and chicks of Adélie Penguins that were kept under regular and frequent surveillance. In this way, causes of mortality and the ages at which it occurred were determined accurately. We used survival analyses to describe the patterns and causes of mortality relative to the ages of the eggs and chicks, and to isolate factors that affect the reproductive success of Adélie Penguins.

METHODS

Study site and animals.—Adélie Penguins are monogamous, laying a single clutch of usually 1–2 eggs at the beginning of each austral summer, within breeding groups called colonies. One of us (L.S.D.) monitored the fates of 858 eggs from 452 nests in 6 colonies of Adélie Penguins comprising H-block in the Northern Rookery (Knox and Ensor 1978), Cape Bird, Ross Island, Antarctica (77°13'10"S, 166°28'30"E) between 23 October 1977 and 24 January 1978. Locations of all 452 nests in the 6 colonies were mapped with reference to painted rock markers and surrounding nests. In 130 (29%) of the 452 breeding pairs, at least one member was banded before breeding began with numbered aluminum-alloy flipper bands for individual identification. Sex was determined from copulatory position or from a combination of behavioral criteria (Sladen 1958: 23–24).

Data collection.—All nests were inspected in sequence daily, usually from 0900 to 1200. Nest contents could be seen if the attending bird altered its position on the nest, or once chicks reached a size that they could no longer be completely covered by their parents; otherwise, a long bamboo pole was used to lift the rears of nesting penguins slightly so that the nest contents could be observed. This minimized disturbance to the birds because, in contrast to other studies (e.g. Penney 1968, Tenaza 1971, the observer never entered the colonies and the penguins remained on their nests. We recorded the dates of egg laying and chick hatching and the cause of any losses of eggs or chicks.

To determine whether there was any adverse effect on reproductive success caused by keeping H-block under frequent surveillance, 39 colonies in A-, B-, C-, and G-blocks of the rookery were used as a control group that was visited only twice during the study (Davis 1982a). Reproductive success in the colonies of H-block was not significantly different from the

reproductive success in the control colonies ($P > 0.05$, Mann-Whitney U -test).

Data analysis.—Times of laying, hatching, and death were measured with an accuracy of ± 12 h. For 1-egg clutches, the age of the egg from laying to hatching or death therefore could be determined with an accuracy of ± 1 day; the same was true for 2-egg clutches where both eggs were lost on the same day, the first was lost before the second was laid, the second was lost after the first hatched, or the eggs were distinguishable by size or color. Otherwise, the age of eggs lost from 2-egg clutches was taken as the average of the ages of the first and second eggs at the time of the death. Time from laying to hatching or demise was determined with an accuracy of ± 1 day for 592 eggs (69.9%), ± 1.5 days for 4 eggs (0.5%), ± 2 days for 14 eggs (1.6%), ± 2.5 days for 192 eggs (22.4%), ± 3 days for 52 eggs (6.1%), and ± 3.5 days for 4 eggs (0.5%).

For chicks, ages from hatching to fledging (defined as being alive on 24 January, when the study ended) or death could be determined with an accuracy of ± 1 day in cases where only one hatched per nest, the first died before the second hatched, both chicks were lost on the same day, or when there was considerable size difference between siblings that enabled them to be identified individually. For other chicks of 2-chick broods, age at death or fledging was taken as the average age of the first and second chicks. Because the period between the hatching of eggs in a 2-egg clutch was usually less than the period between their laying, ages of chicks were known with greater accuracy. Time from hatching to fledging or death was known to ± 1 day for 366 chicks (75.9%), ± 1.5 days for 72 chicks (14.9%), ± 2 days for 32 chicks (6.6%), ± 2.5 days for 10 chicks (2.1%), and ± 3 days for 2 chicks (0.4%).

Survival was analyzed by evaluating the time elapsed between laying or hatching (the starting event) and death due to a particular cause or causes (the terminal event). The probabilities of an egg or chick succumbing to any particular cause were calculated for 2-day intervals from laying or hatching. For the purposes of the analysis, added or infertile eggs were deemed to have been lost in the first 2-day interval immediately after laying. Causes of death other than those under consideration as the terminal event, and eggs that hatched or chicks that fledged, were treated as censored observations (cases where the terminal event did not occur). Survival estimates were based on the survival times of both censored and uncensored (cases where the terminal event occurred) observations. To make maximum use of censored data, we assumed that eggs and chicks censored during a 2-day interval were lost, on average, halfway through that interval. Thus, the number exposed to risk of the terminal event during a 2-day interval was the number entering the interval minus one-half of the number censored during that inter-

TABLE 1. Mean dates of laying (all dates in November), causes of mortality, survival, reproductive success, and nest ratio for colonies of Adélie Penguins in H-block.

	Colony						Total
	H1	H2A	H2B	H3	H4A	H4B	
Laying dates ($\bar{x} \pm SD$)							
First egg of 2-egg clutch	12.7 \pm 3.4 (n = 30)	12.1 \pm 3.7 (n = 20)	13.2 \pm 3.5 (n = 61)	12.1 \pm 3.0 (n = 37)	11.5 \pm 2.4 (n = 31)	11.8 \pm 3.3 (n = 217)	12.1 \pm 3.3 (n = 396)
Second egg of 2-egg clutch	15.7 \pm 3.4 (n = 30)	15.2 \pm 3.6 (n = 20)	16.1 \pm 3.5 (n = 61)	15.2 \pm 3.0 (n = 37)	14.7 \pm 2.5 (n = 31)	15.0 \pm 3.1 (n = 217)	15.2 \pm 3.2 (n = 396)
1-egg clutch	14.8 \pm 3.3 (n = 6)	17.0 \pm 7.1 (n = 2)	20.9 \pm 6.9 (n = 7)	16.8 \pm 6.0 (n = 6)	16.8 \pm 4.1 (n = 5)	15.7 \pm 5.7 (n = 25)	16.6 \pm 5.6 (n = 51)
Eggs							
Total laid	66	42	135	80	67	468	858
Total lost	26	5	48	43	32	222	376
Lost to skuas	4	0	8	7	22	116	157
Deserted (mate did not return)	14	3	30	30	6	48	131
Addled or infertile	6	2	6	1	2	40	57
Broken	1	0	4	1	0	14	20
Lost to other causes	1	0	0	4	2	4	11
Chicks							
Total hatched	40	37	87	37	35	246	482
Total lost	14	11	24	28	23	77	177
Lost to skuas	10	9	10	17	18	48	112
Died of starvation	3	2	14	11	3	29	62
Lost to other causes	1	0	0	0	2	0	3
Survived	26	26	63	9	12	169	305
Reproductive success (%)	39.4	61.9	46.7	11.3	17.9	36.1	35.6
Nest ratio (central : peripheral)	0.94	0.83	0.97	0.83	0.30	0.66	0.71

val. This was used to compute the hazard function, i.e. the probability that an individual egg or chick that has survived to the beginning of a 2-day interval will die because of a terminal event within that interval. Survival distributions from different samples (number of samples = K) were compared statistically using an extension of the nonparametric Kruskal-Wallis test (Lee and Desu 1972). The statistic, D , is asymptotically distributed as a Chi-square distribution with $K - 1$ degrees of freedom under the null hypothesis that the samples are from the same survival distribution (Breslow 1970, Lee and Desu 1972). The larger the D statistic, the more likely the samples come from different survival distributions. All computations were made using the SPSS program "survival" (Hull and Nie 1979).

The following definitions were used to classify factors that may influence breeding success. *Central nest*: a nest surrounded by six other nests (Tenaza 1971). This results in there being at least one nest site between a central nest and the outside of the colony.

Peripheral nest: a nest exposed to the colony edge (Penney 1968, Spurr 1972). This occurs if there are fewer than six surrounding nests (Tenaza 1971). *Early breeders*: pairs whose first egg is laid before the mean date for first eggs (MDFE). *Late breeders*: pairs whose first egg is laid after the MDFE.

RESULTS

Of the 452 breeding pairs, 51 (11.3%) laid only one egg, 396 (87.6%) laid two eggs, 3 laid a third egg after losing their first within 24 h, and 2 laid three-egg clutches without losing an egg before the completion of laying. Mean date of laying (± 1 SD) was 12.6 (± 3.8) November ($n = 452$) (Table 1). The interval between first and second eggs in 2- and 3-egg clutches was usually 3 days (64.2%), with 97.8% being 2-4 days (range = 1-8, $n = 401$). Incubation periods

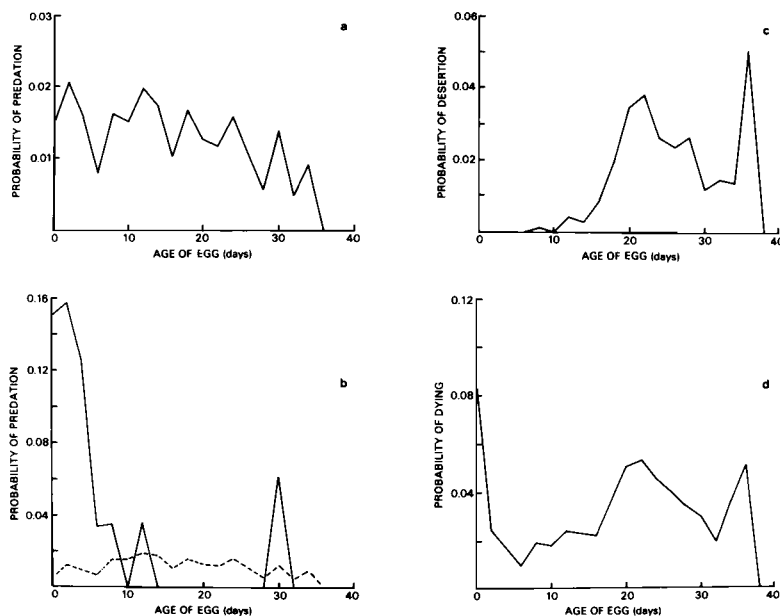


Fig. 1. Hazard functions for a sample of 858 Adélie Penguin eggs showing the probability that eggs that survive to the beginning of each 2-day interval will die within that interval due to (a) skua predation, (b) skua predation on 1-egg (solid line) and 2-egg (dashed line) clutches, (c) desertion because a mate does not return, and (d) all causes of mortality.

were 34.5 ± 1.7 days for 1-egg clutches (range = 31–37, $n = 14$), 35.2 ± 1.2 days (range = 32–39, $n = 192$) for first eggs of 2-egg clutches, and 33.7 ± 1.1 days (range = 32–38, $n = 192$) for second eggs of 2-egg clutches. Of the 858 eggs laid in H-block, 482 hatched, giving a hatching success of 56.2%. Fledging success for chicks was 63.3%, with 305 surviving until the end of the study on 24 January. Overall reproductive success (laying to fledging) was 35.6%, although reproductive success was variable between colonies (Chi-square test, $\chi^2 = 49.2$, $P < 0.01$), ranging from 11.3 to 61.9%.

Egg survival.—Egg losses due to predation by skuas occurred throughout the incubation period. The hazard to eggs from skuas decreased slightly with time (Fig. 1a; $r = -0.58$, $P < 0.05$), so that eggs that were successfully protected from skuas during the early stages of incubation were at less risk of being taken during the later stages. Eggs in peripheral nests were more susceptible to predation (27.1%, 136/501) than those in central nests (5.9%, 21/357) ($D = 56.6$, $df = 1$, $P < 0.001$). Survival of eggs in central nests was the same for all colonies ($D = 4.3$, $df = 4$, $P > 0.3$).

Early breeders were less likely to lose their

eggs to skuas (15.5%, 76/489) than were late breeders (22.0%, 81/369) ($D = 7.3$, $df = 1$, $P < 0.01$). Early breeders accounted for 239 of 367 eggs (65%) laid in central nests. Egg survival against predation did not differ for early and late breeders in central nests ($D = 0.5$, $df = 1$, $P > 0.4$).

Eggs from 1-egg clutches (41.2%, 21/51) were more likely to be taken by skuas than eggs from 2-egg clutches (16.7%, 132/792) (Fig. 1b; $D = 34.0$, $df = 1$, $P < 0.001$). Although 66.7% (34/51) of 1-egg clutches were laid in peripheral nests, the greater risk to 1-egg clutches was independent of their nest location, as they were more likely to lose their eggs to skuas in both central ($D = 25.9$, $df = 1$, $P < 0.001$) and peripheral nests ($D = 17.4$, $df = 1$, $P < 0.001$). Survival of 1-egg clutches did not differ with time of laying ($D = 2.4$, $df = 2$, $P > 0.3$). One-egg clutches were most vulnerable to skuas during the first 4 days of incubation (Fig. 1b).

Predation differed among colonies ($D = 46.6$, $df = 5$, $P < 0.001$), with skuas taking more eggs from colonies H4A and H4B than from other colonies (Table 1). The proportion of peripheral nests was greatest in colonies H4A and H4B (Table 1), but even so, peripheral nests in H4A

TABLE 2. Summary of the effects of factors on the causes of mortality of eggs and chicks of Adélie Penguins.

Cause of mortality	Per- cent lost	Per- centage of losses	Period of risk	Peak risk (days old)	Factor ^a				
					Nest lo- cation	Time of breed- ing	Clutch size	Colony	Brood size
Eggs									
Skua predation	18.3	41.8	Day 0 to hatching	2-4	+	-	+	+	
Desertion	15.3	34.9	Day 8 to hatching	22-24	-	+	+	+	
All causes	43.8	100.0	Day 0 to hatching	0-2	+	+	+	+	
Chicks									
Skua predation	23.2	63.3	Days 0-30	10-12	+	-	-	+	-
Starvation	12.9	35.0	Days 4-24	6-8	-	-	-	-	-
All causes	36.7	100.0	Days 0-30	6-8	+	-	-	+	-

^a "+" = significant effect, "-" = no significant effect.

lost 41.5% (22/53) and those in H4B lost 35.6% (100/281) of their eggs to skuas, which was significantly more ($D = 35.3$, $df = 1$, $P < 0.001$) than the other colonies (8.4%, 14/167). This points to variations among the skuas in the degree to which they either relied on or were able to exploit the source of penguin eggs within their territories. All of colony H4A and part of H4B fell within the territory of a skua pair (433/042) that was particularly adept at stealing eggs.

Of the 858 eggs laid, 139 (16.2%) were deserted. Desertions, in those pairs where one or both birds were banded or otherwise distinguishable (76 eggs from 43 nests), resulted unequivocally from one mate failing to return in time to relieve the other on the nest (see Davis 1982a). Almost all desertions involving unbanded and undistinguishable pairs could be attributed to the same cause, as they were similar in character to desertions from nests where a mate was known not to have returned in time to relieve the nest (i.e. the incubating bird had been on the nest for a longer than normal period). Typically, penguins whose mates were overdue became flighty (i.e. inclined to leave the nest when approached by an observer) during the few days immediately prior to the desertion. Thirty-five desertions involving 55 eggs fitted this pattern, and the time from the completion of laying until desertion of those 35 clutches where the mate was presumed not to have returned ($\bar{x} = 22.9 \pm 5.9$ days) was the same as for the 43 desertions where the mate was known not to have returned ($\bar{x} = 22.5 \pm 4.6$ days) (Student's t -test, $t = 0.36$, $df = 76$, $P > 0.7$). In all, 131 eggs were lost because the in-

cubating bird was not relieved by its mate, and these comprised 35% of all egg losses. A further 5 eggs were deserted because their nests were flooded with meltwater from snow, and for 3 eggs the cause of desertion could not be ascertained.

The risk of desertion for the egg was virtually nil until the egg was 16 days old, then increased rapidly, reaching a peak at 22 days (Fig. 1c). Thereafter, the risk decreased until the egg was 34 days old, the time of hatching. Eggs incubated longer than the normal incubation period had a high chance of being deserted.

The loss of eggs due to desertion was not significantly different in peripheral nests (16.6%, 83/501) and in central nests (13.4%, 48/357) ($D = 3.0$, $df = 1$, $P > 0.05$). However, the likelihood of an egg being deserted was affected by the time the parents bred ($D = 38.6$, $df = 3$, $P < 0.001$). Very late breeders (those that began laying 1 SD after the MDFE) were the most likely to lose their eggs (29.5%, 28/95). Proportionately twice as many eggs from late breeders were deserted (21.4%, 79/369) compared with those of early clutches (10.6%, 52/489). Eggs from 1-egg clutches (21.6%, 11/51) were more prone ($D = 6.19$, $df = 1$, $P < 0.05$) to be deserted than those from 2-egg clutches (14.9%, 118/792). The likelihood of desertions was not the same for all colonies ($D = 36.8$, $df = 5$, $P < 0.001$), and the three colonies in which desertions were most prevalent (Table 1: H1, H2B, H3) had a higher proportion of eggs belonging to late breeders (52.7%, 148/281) than did the other colonies (38.3%, 221/577).

The hazard function for eggs varied over the

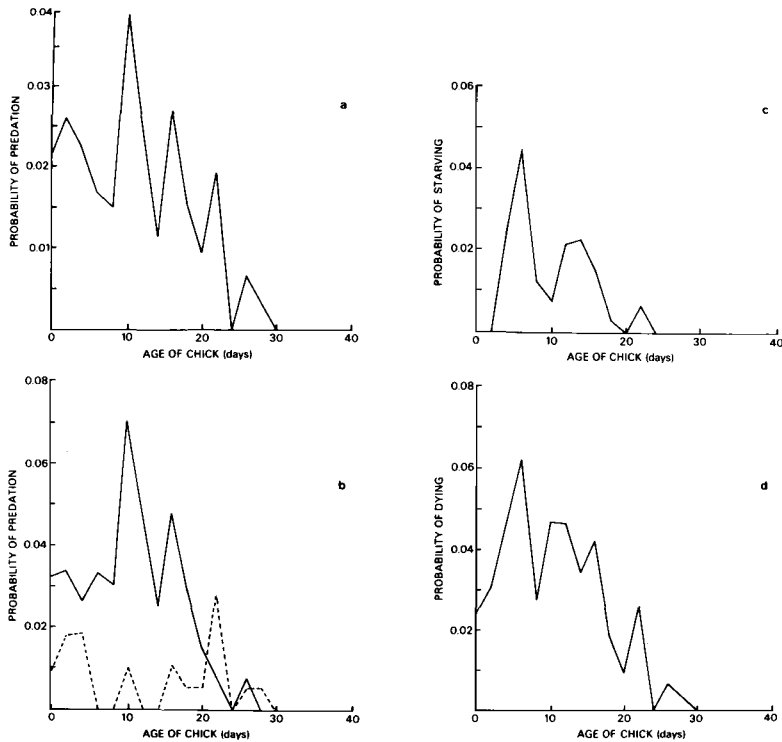


Fig. 2. Hazard functions for a sample of 482 Adélie Penguin chicks showing the probability that chicks that survive to the beginning of each 2-day interval will die within that interval due to (a) skua predation, (b) skua predation on peripheral (solid line) and central (dashed line) nests, (c) starvation, and (d) all causes of mortality.

entire incubation period (Fig. 1d). The likelihood of an egg being lost was greatest during the first 2 days (either to skuas or through being added or infertile) and peaked again at 22 days, when desertions occurred most frequently. Eggs had better prospects of surviving incubation through to hatching if they were from central nests ($D = 10.4$, $df = 1$, $P < 0.005$), belonged to early breeders ($D = 14.9$, $df = 1$, $P < 0.001$), and were from 2-egg clutches ($D = 26.6$, $df = 1$, $P < 0.001$) (Table 2).

Chick survival.—Chicks were at risk to predation by South Polar Skuas until they were 30 days old (Fig. 2a). The risk was greatest at 10–12 days of age and declined sharply after 22 days. The likelihood of a chick being taken by skuas was not affected by the timing of breeding of its parents ($D = 2.3$, $df = 3$, $P > 0.5$), whether it had hatched from a 1-egg or 2-egg clutch ($D = 0.1$, $df = 1$, $P > 0.7$), or whether it was from a 1-chick or 2-chick brood ($D = 0.3$, $df = 1$, $P > 0.5$). By contrast, chicks in peripheral nests were much more prone to predation

by skuas (30.0%, 76/253) than were chicks in central nests (10.0%, 23/229) (Fig. 2b; $D = 33.0$, $df = 1$, $P < 0.001$). Predation success differed among colonies ($D = 57.3$, $df = 5$, $P < 0.001$), in both central ($D = 37.9$, $df = 5$, $P < 0.001$) and peripheral ($D = 40.5$, $df = 5$, $P < 0.001$) nests; colonies H3 and H4A lost the greatest proportion of their chicks to skuas (Table 1). Part of colony H3 also fell within the territory of the skua pair 433/042.

The likelihood of dying of starvation was nil during the first 4 days of a chick's life, but reached a sharp peak at 6–8 days of age (Fig. 2c). The risk remained substantial until 16 days, then declined rapidly, until by 24 days it was again zero. The likelihood of starvation was not influenced by the timing of breeding ($D = 2.7$, $df = 3$, $P > 0.4$), clutch size ($D = 0.3$, $df = 1$, $P > 0.6$), brood size ($D = 0.2$, $df = 1$, $P > 0.6$), or nest location ($D = 3.7$, $df = 1$, $P > 0.05$). The pattern of starvation was similar for all colonies ($D = 3.6$, $df = 4$, $P > 0.4$), except H3 (Table 1).

Overall, chicks were at greatest risk of dying during the first 18 days of their lives (Fig. 2d). Chicks older than 30 days were not likely to die before they fledged. Survival of chicks was not influenced by the time the parents bred ($D = 5.3$, $df = 3$, $P > 0.1$), clutch size ($D = 0.0$, $df = 1$, $P > 0.9$), or brood size ($D = 0.0$, $df = 1$, $P > 0.8$). Nest location ($D = 34.0$, $df = 1$, $P < 0.001$) and colony ($D = 61.2$, $df = 5$, $P < 0.001$) did affect the survival of chicks (Table 2).

Factors affecting reproductive success.—Survival of eggs and chicks from laying to fledging was similar for early and late breeders (Table 3). The incidence of predation was highly correlated with the ratio of central to peripheral nests within a colony (Table 1; $r = 0.98$, $P < 0.001$), which was determined by the size and shape of the colony. The reproductive success of central nesters was nearly double that of peripheral nesters, and, similarly, eggs from 2-egg clutches were twice as successful as eggs from 1-egg clutches (Table 3).

DISCUSSION

In the medical sciences, survival analysis is used extensively to identify critical periods of risk, and by comparing the patterns of risk under different conditions, so isolate the factors important for survival (e.g. Blackwood et al. 1977). Here we have used survival analysis to identify when Adélie Penguin eggs and chicks are susceptible to differing causes of mortality, and what factors influence survival with respect to those causes.

Two major causes were responsible for the mortality of eggs and chicks of Adélie Penguins (Table 2). Predation by skuas was the major cause of loss for both eggs and chicks. Previously, skuas have been reported to be a main source of chick mortality (Sapin-Jaloustre 1960, Taylor 1962, Spurr 1975) but have been dismissed as a significant source of egg losses (Taylor 1962, Young 1963, Maher 1966) because they are regarded chiefly as scavengers (Sladen 1958, Trillmich 1978). Eggs were susceptible to predation at all times throughout the incubation period (Fig. 1a). Chicks, on the other hand, were most vulnerable to skuas during the first 22 days after hatching, which corresponds to the guard stage (Davis 1982b), when they are guarded at the nest by one parent. Older chicks are left unguarded, and in the absence of adults form creches, the creche stage. Creche stage

TABLE 3. Comparison of survival of Adélie Penguin eggs to fledging by time of breeding, nest location, and clutch size.

	No. of eggs laid	No. fledged ^a	Percent survival	P ^b
Time of breeding				
Early	489	194	39.7	NS
Late	369	124	33.6	
Nest location				
Central	357	182	51.0	**
Peripheral	501	136	27.1	
Clutch size ^c				
One egg	51	10	19.6	*
Two eggs	792	301	38.0	

^a Does not include 12 chicks lost to skuas.

^b NS = nonsignificant ($P > 0.05$), * = $P < 0.05$, ** = $P < 0.001$; G-test with William's correction.

^c Does not include 5 three-egg clutches.

chicks were vulnerable up to 30 days old, by which time they weighed an average of 3 kg and were probably too big for skuas to kill under normal circumstances (Davis 1982b).

The most obvious factor influencing the survival of eggs and chicks against skua predation was nest location. Predation occurred mainly on peripheral nests, as was observed in other studies of Adélie Penguins (Taylor 1962, Spurr 1975). Once chicks reached the creche stage, when chicks from central and peripheral nests mixed together, the progeny of peripheral nesters ceased to be at greater risk (Fig. 2b). Central nest locations also correlate with higher reproductive success in Black-legged Kittiwakes (*Rissa tridactyla*; Coulson 1968) and gulls (Dexheimer and Southern 1974, Ryder and Ryder 1981, Pugsek and Diem 1983). The size and shape of the colony influenced survival from skuas. Nevertheless, predation was higher in some colonies regardless of the proportion of peripheral nests.

Timing of breeding did not directly influence predation of either eggs or chicks, although early breeders gained a greater proportion of central nests. This contradicts Spurr's (1972) suggestion that chicks of very early breeders are more susceptible to skua predation. However, clutch size, which is highly correlated with age and experience of the breeders, did affect the likelihood of egg loss. One-egg clutches are laid almost exclusively by young breeders, i.e. 3-5-year-old females (Reid 1968). The greater susceptibility of 1-egg

clutches was independent of their nest location, and they were most vulnerable to skuas during the first 4 days of incubation (Fig. 1b), suggesting that those breeders were either less able to defend their eggs or invested less effort in defense. Young breeders invest less than older breeders in defending the nest from predators in gulls (Pugesek 1983) and sparrows (Smith et al. 1984). One-egg clutches that survived the initial third of incubation were not more susceptible to subsequent skua predation, and neither were chicks that hatched from 1-egg clutches. This implies that the inexperience of the breeders did not affect the survival prospects of eggs and chicks once the parents had demonstrated an initial ability to fend for the eggs. Spurr (1972) also found chicks from 1-egg clutches suffered mortality similar to those from 2-egg clutches.

Desertions and starvations were the second-most important cause of egg and chick losses, respectively (Table 2). Most desertions occur when females do not return in time to relieve males from the first incubation spell. Our results were contrary to Young's (1963) assertion that many eggs are subject to desertion during the first week of incubation. By contrast, newly hatched chicks can survive for an average of 6.4 days (range = 5.5–8) on their yolk reserves (Reid and Bailey 1966). The greatest likelihood of starvation was at 6–8 days old (Fig. 2c), which implies that the affected chicks were not fed in the first week after hatching. Starvations occur when a parent fails to return to the nest in time, leaving its mate to guard the nest without food to feed the chicks. Starvations that occur as a result of chicks not being fed after hatching often are due to males not returning from the second incubation spell (Davis 1982a). Once emancipated from guard duties, one parent could feed the chicks in the absence of its mate, so that starvation ceased to be a risk after the end of the guard stage (Fig. 2c). That some chicks starve has led to the unwarranted conclusion that food must be limiting (Maher 1966, Ainley and Schlatter 1972), instead of attributing the cause to inadequate timing of nest relief (Davis 1982a). Spurr (1975) also found that chicks starved only during the guard stage, and concluded that chicks were not dying because of a shortage of food at sea.

Late breeders and those laying 1-egg clutches were most likely to desert. The latter is contrary to Sapin-Jaloustre's (1960) impression that

1- and 2-egg clutches were equally likely to be deserted, and suggests that timing ability improves with age or experience. Young Adélie Penguins tend to have the smallest clutches and the least normal incubation routines (Ainley et al. 1983). Desertions resulting from a mate not returning in time, or from improper incubation routines, were responsible for the majority of egg losses in young breeding Adélie Penguins (3–7 years old) and their mates (Ainley et al. 1983). Similarly, in kittiwakes newly formed pairs do not coordinate their incubation pattern as well as established pairs do (Coulson 1966). Late breeding can be caused by asynchronous arrival of pairs at the rookery at the beginning of the breeding season. Courtship usually takes about 11 days (Davis 1982a), and males that are ashore for much longer than that before laying is completed have less fat reserves available for the first incubation spell (Johnson and West 1973). For such late-breeding pairs, the timing of nest relief becomes even more critical. To some extent, however, timing of breeding and clutch size are interrelated, as young breeders (those that lay most 1-egg clutches) tend to be less synchronous in their arrival than older pairs (LeResche and Sladen 1970). Starvation was not influenced strongly by any of the factors studied (Table 2), indicating that late breeders and breeders laying 1-egg clutches that coordinated their nest-relief pattern throughout the incubation period were able to continue to do so as successfully as earlier and older breeders.

The interrelationship of the factors that influence reproductive success makes it difficult to assess their effects separately (Birkhead et al. 1983). In Mute Swans (*Cygnus olor*), reproductive success is most significantly associated with clutch size, which in turn is affected by the timing of breeding and the experience of the pair (Birkhead et al. 1983). Coulson (1968) argued that nest location was of prime importance to kittiwake reproductive success, creating intense competition for central nests. By contrast, Pugesek and Diem (1983) found that parental age was the most important determinant of reproductive success in California Gulls (*Larus californicus*) and that it was only the covariance of nest location with parental age that made the nest location appear to influence breeding performance. A similar suggestion has been made for Adélie Penguins (Ainley et al. 1983). However, Adélie Penguins in peripheral

nests increase their reproductive success in subsequent seasons only if they move to a central nest, and central nesters that move to peripheral locations suffer reduced reproductive success (Spurr 1975). We found that peripheral nests of both 1-egg and 2-egg clutches were more susceptible to predation than their central counterparts, so that nest location has a major effect on breeding success that is independent of the age of the breeders. The likelihood of getting a peripheral nest will in part be determined by colony size and shape, yet, while peripheral breeders may do less well than central breeders, they probably do much better than if they nested in isolation from the colony (Gotmark and Andersson 1984). From our analysis, we conclude that timing of breeding and clutch size (age) are important for the early survival of the egg, whereas nest location has a major influence on survival through to the end of the guard stage. Adélie Penguin eggs have better prospects of producing fledglings when they are laid in central nests and laid in 2-egg clutches.

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