# EFFECTS OF HATCHING ORDER, SIBLING ASYMMETRIES, AND NEST SITE ON SURVIVAL ANALYSIS OF JACKASS PENGUIN CHICKS

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ABSTRACT.—We used survival analysis to examine the fates of Jackass Penguin (*Spheniscus demersus*) chicks on Dassen Island, off the west coast of South Africa. There were two distinct phases of chick loss. The first, when chicks were 0–34 days old, involved losses primarily due to burrow collapse, exposure and drowning, and accidental death in the nest. This mortality was influenced strongly by nest-site characteristics. Overall reproductive success was lowest in open nests, intermediate in burrows, and highest in rock nests. The probability of chick death due to flooding was highest for burrows in shell/guano conglomerate, whereas the risk of burrow collapse was highest in sand. Burrows in high-density colonies had a greater likelihood of collapsing after heavy rain than burrows in low-density areas. The second phase occurred 42–90 days after hatch, when losses were almost entirely due to starvation. Comparisons of survival in control and experimental nests with varying degrees of sibling asymmetry indicate that it is the extent of hatching asynchrony that affects the ability of the smaller sibling to compete for food and that will produce sibling differences in the risk of starvation. Chicks in two-chick control nests starved at higher frequencies than chicks in less asynchronous experimental broods. *Received 24 April 1990, accepted 17 December 1990.*

STUDIES of the breeding success of colonial seabirds may be hampered by the complexity with which many factors influence reproductive success (Davis and McCaffrey 1986). In particular, the inability to identify specific causes of chick mortality limits our knowledge of the factors that influence breeding failure.

Recent studies of the Jackass Penguin (*Spheniscus demersus*) provided estimates of breeding success (Frost et al. 1976a, Cooper 1980, Randall and Randall 1981, Randall 1983, LaCock et al. 1987) without identifying specific causes of mortality or the timing of losses. No published study of the Jackass Penguin has considered either the timing of separate causes of chick mortality or the effect of sibling asymmetries on the probability of survival.

We used survival analysis techniques (Davis and McCaffrey 1986) to (1) quantify the causes and timing of prefledging Jackass Penguin chick mortality; (2) investigate the effect of hatching order, chick number, and sibling size asymmetries on chick loss in natural asynchronous nests; (3) compare chick survival in natural asynchronous nests and experimental nests having different degrees of asynchrony; and (4) examine the influence of nest site on chick mortality.

## METHODS

*Study area and animal.*—Jackass Penguins breed on small islands off the west and east coasts of southern Africa (Frost et al. 1976a). A clutch of 1–2 eggs is laid in a simple nest bowl in an excavated burrow beneath rocks or low-lying vegetation, or in an open nest-scrape. Fewer than 1% of clutches have only a single egg (P. J. Seddon and Y. van Heezik unpubl. data, Williams and Cooper 1984). The first-laid egg (A-egg) of a clutch is on average 4.6 g heavier (range 0–12 g) and hatches 2.1 days earlier (range 1–4 days) than the second-laid egg (B-egg) (Williams and Cooper 1984). We found differential egg-size and hatching asynchrony produce mean sibling mass differences of 54.6 g at the hatching of the B-egg. Although breeding may occur at any month of the year, a west coast winter breeding peak (May to September) corresponds to high food availability, lowered ambient temperatures, and high chick survival (Cooper 1980, Wilson 1985). Hatching occurred between June and August. We monitored the fates of 253 chicks from 143 nests on Dassen Island (32°25'S, 18°05'E) between 15 June and 3 November 1989.

*Data collection.*—We inspected all nests in sequence daily between 0900 and 1400. We weighed chicks at hatching and at 5-day intervals until fledging or demise. We recorded the dates of chick hatching (chick completely clear of the shell), and the dates and causes of chick losses. We recorded within-clutch hatching order and identified individual chicks by color-mark-

ing (1–10 days), by temporary velcro flipper tags (11–60 days), and by permanent stainless steel flipper bands (>60 days). Nest sites were classified at the time of chick hatching as burrows in sand, burrows in shell/guano conglomerate, beneath rocks (rock nests), or exposed with no overhead cover (open nests).

To determine whether frequent surveillance of the study nests had an adverse effect on chick survival, we visited a control group for disturbance effects at approximately 14-day intervals. Survival rates of individual chicks from the normal asynchronous control (63% losses) and the undisturbed control (58% losses) were not significantly different (Chi-square = 0.23, df = 1, n = 219 chicks, P > 0.05). We conclude that frequent visits had no effect on chick survival.

*Chick transfers.*—By interchanging newly hatched chicks between nests, we established 57 experimental broods with different degrees of size asymmetry. We established 39 nests with *similarly sized* siblings (mean weight difference at hatching of the second chick was 2.5 g; range was 0–5 g). We defined 8 nests with *small differences* in sibling size (mean weight difference 9.9 g, range 6–20 g). Finally in 10 nests with large differences in sibling size, we used increased sibling mass differences to simulate *extended asynchronous* hatching (mean weight difference 161 g, range 62–260 g). An unmanipulated control group consisted of 53 normal asynchronous two-chick nests (mean sibling weight difference 54.6 g, range 11–150 g) and 33 one-chick nests in which only one egg was laid (n = 1), one egg was lost during incubation (n = 16), or one egg was infertile (n = 16).

*Data analysis.*—Times of hatching and fledging or death were measured to ±12 h; ages of individual chicks at fledging or demise were therefore determined to ±1 day. We recognized several causes of chick death. (1) Starvation: chicks found dead after prolonged or rapid weight loss presumably starved. (2) Predation: when chicks <10 days old disappeared, or carcasses bearing wounds consistent with attack by Kelp Gulls (*Larus dominicanus*), Sacred Ibis (*Threskiornis aethiopicus*), or feral domestic cats (*Felis lybica*) were recovered, they were presumably taken by a predator. (3) Exposure: death occurred after exposure to rain and wind, or drowning in flooded nest bowls. (4) Accidental: death not obviously associated with any of the previous causes, often crushing by parents of young chicks, was considered accidental. (5) Collapse: some deaths were due to smothering in a collapsed burrow. Chicks that did not succumb to these causes were categorized as those that fledged and those that could not be located after wandering from the nest site after approximately 30 days of age.

*Survival.*—To analyze survival of chicks we evaluated the length of time from hatching to a response. Responses were either "censored" (when death did not occur: fledging or disappearance) or "uncensored" (when death occurred). Survival estimates were based on the survival times of both censored and uncensored cases. The survivor function is the probability that, for any specified survival time interval, an individual will survive at least that long. We estimated the survivor function for 4-day intervals beginning at hatching. We represented survival graphically as either the cumulative proportion of chicks that survived to the $i$th interval as an estimate of the *survivor function*, or as a *hazard function*, the instantaneous rate of failure at a specified time, given that the chick survived to at least that time (Davis and McCaffrey 1986).

Survivor function distributions from different samples (number of samples = K) may be compared by the calculation of a nonparametric test statistic, asymptotically distributed as Chi-square with $K - 1$ degrees of freedom. The larger the test statistic, the more likely the samples came from different survival distributions. We made all survivor function comparisons between groups with the Tarone-Ware test statistic (*TW*) (Tarone and Ware 1977). We used the BMDP program "1L Life Tables and Survivor Functions" (Dixon 1988) to make all computations.

## RESULTS

*Survival of control chicks.*—Chicks in unmanipulated control nests faced the greatest risk of dying (due to drowning, exposure, smothering in a burrow collapse, or crushing by the attending adult or other accidental causes) in the first 10 days after hatching (Fig. 1a). This risk decreased sharply after 10 days, and by 38 days it was nil (Fig. 1a). Chicks risked predation until 30 days of age. The probability of predation was greatest at 10 days of age, and then it decreased gradually (Fig. 1a). The risk of starvation increased from 4 days post-hatch to an initial peak between 14 and 18 days. Subsequently it increased rapidly after 38 days to a maximum at 86 days (Fig. 1b).

Overall, chicks were at greatest risk of dying during the first 10 days post-hatch (Fig. 1c). Early death decreased after hatching and no deaths occurred between 36 and 40 days. After 40 days the probability of death by starvation increased sharply and was the single greatest cause of chick mortality between 40 days and fledging (Fig. 1). In total, starvation accounted for 45% (39/87) of all control chicks losses (Table 1). Chicks that survived longer than 92 days generally fledged successfully.

*Brood size.*—There was no difference in overall mortality (Tarone-Ware test, $TW = 0.02$, df $= 1, P > 0.8$), between one- and two-chick nests in the control group, nor in mortality due to starvation ($TW = 3.3$, df $= 1, P = 0.07$), exposure
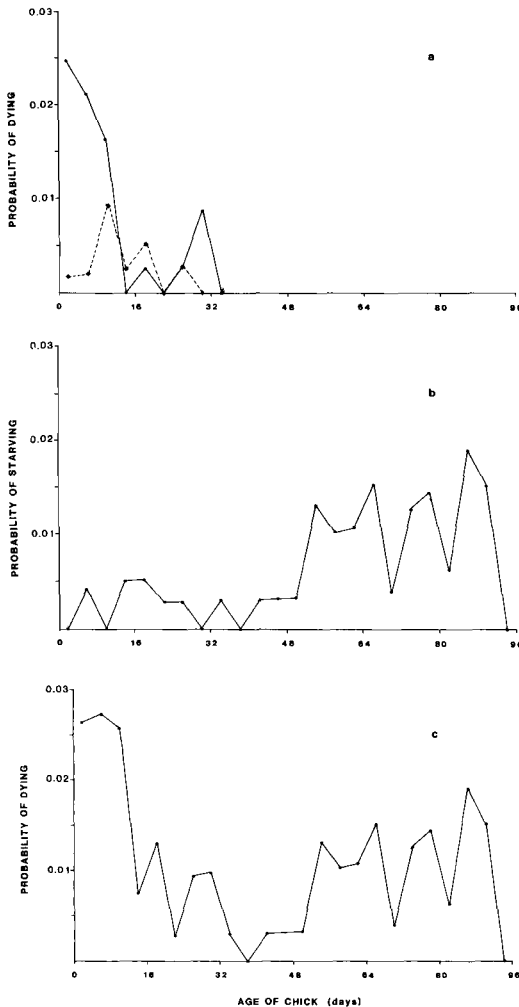
Fig. 1. Hazard functions for 139 Jackass Penguin chicks, showing the probability that chicks that survive to the beginning of each 4-day interval will die within that interval due to (a) exposure, burrow collapse, or other accidental causes (solid line), or predation (dashed line); (b) starvation; and (c) all causes.

or accidental nestling death ($TW = 0.1$, df $= 1$, $P > 0.7$). There was also no difference in the probability of mortality due to any cause ($TW = 0.9$, df $= 1$, $P > 0.3$), nor mortality due to starvation ($TW = 1.3$, df $= 1$, $P > 0.2$) between A-chicks of two-chick nests and singleton chicks, and no difference in overall mortality between singletons and B-chicks ($TW = 1.3$, df $= 1$, $P > 0.2$). The likelihood of death by starvation, however, differed significantly between B-chicks and singletons (Fig. 2) ($TW = 5.7$, df $= 1$, $P < 0.05$).

Of B-chicks 36% (19/53) starved, compared with 12% (4/33) of single chicks (Table 2).

*Hatching order and sibling asymmetries.*—There was no difference in the overall probability of starvation of A-chicks vs. B-chicks in control nests ($TW = 3.4$, df $= 1$, $P > 0.05$). However, when considering nests at which starvation was the only cause of mortality of either A- or B-chicks, or both chicks ($n = 15$ nests), then B-chicks were significantly more likely to starve ($n = 15$, 100%) than their larger A-chick siblings ($n = 10$, 66%) (Fisher exact probability test, $P = 0.02$). Differences between siblings due to differential egg size, as approximated by the "small difference" manipulation, did not produce differences in overall morality ($TW = 0.03$, df $= 1$, $P > 0.8$). The risk of starvation was not significantly different between control A-chicks and similarly sized chicks ($TW = 0.9$, df $= 1$, $P > 0.3$), but differed between control B-chicks and similarly sized chicks ($TW = 6.6$, df $= 1$, $P < 0.05$). The timing of losses of similarly sized chicks showed the same pattern as that of control chicks (Figs. 1c and 3), with a high initial risk of mortality primarily due to causes other than starvation. Between 50 and 90 days of age starvation was the cause of all similarly sized chick deaths (Fig. 3). The likelihood of starving for all control chicks in two-chick nests (Table 2) was significantly greater than for similarly sized chicks ($TW = 4.1$, df $= 1$, $P < 0.05$) or small-difference chicks ($TW = 3.99$, df $= 1$, $P < 0.05$) (Fig. 4). No differences existed between nests of small-difference chicks vs. nests of similarly sized chicks ($TW = 0.97$, df $= 1$, $P > 0.3$) (Fig. 4). The mortality of extended asynchronous chicks differed from that of all three other groups (Table 1) (control vs. extended asynchronous, $TW = 7.2$, df $= 1$, $P < 0.01$; small difference vs. extended asynchronous, $TW = 7.1$, df $= 1$, $P < 0.01$; same sized vs. extended asynchronous, $TW = 7.7$, df $= 1$, $P < 0.01$) (Fig. 4). This was due to the high probability of death by starvation of extended asynchronous B-chicks compared with A-chicks ($TW = 8.6$, df $= 1$, $P < 0.005$), with 80% (8/10) of B-chicks starving to death (Table 2).

*Nest site.*—Nests in control, similarly sized, and small-difference groups were combined and reclassified according to nest type (burrow, rock, open) to examine causes of mortality unrelated to sibling asymmetries. Differences existed between the control and manipulated groups in chick loss due to burrow collapse and predation

TABLE 1. Mortality, survival, and fledging success in control and experimental groups of Jackass Penguin chicks. Experimental groups are similarly sized siblings, differently sized siblings, and extended asynchronous siblings.

| | | Experimental | | |
|---|---|---|---|---|
| | Control | Similar size | Different size | Extended asynchrony |
| Total no. hatched | 139 | 78 | 16 | 20 |
| Total no. lost | 87 | 31 | 5 | 14 |
| Losses (%) | | | | |
| Burrow collapse | 13 | 0 | 0 | 0 |
| Exposure/drowning | 8 | 13 | 0 | 0 |
| Accident | 20 | 13 | 20 | 7 |
| Predation | 11 | 0 | 0 | 7 |
| Starvation | 45 | 71 | 60 | 79 |
| Disappearance | 3 | 3 | 20 | 7 |
| Fledging success (%) | 37.4 | 60.3 | 68.8 | 30.0 |

(Table 1). However, a high proportion of control burrows were in sandy substrate (Table 3), and the result was not due to sibling size asymmetries.

The likelihood of mortality due to nest-site-related causes differed for chicks in burrows and chicks in rock nests ($TW = 10.5$, df = 1, $P < 0.005$), in that the risks of collapse ($TW = 4.9$, df = 1, $P < 0.05$) and exposure ($TW = 3.9$, df = 1, $P < 0.05$) were greater in burrows (Table 3). The risk of dying differed for chicks in open nests compared with those in rock nests ($TW = 5.8$, df = 1, $P < 0.05$), but not compared with those in burrows ($TW = 0.002$, df = 1, $P > 0.9$). The percentage of chicks lost to nest-related causes was highest in open nests, intermediate in burrows, and lowest in rock nests (Table 3).

Different substrata were used for burrows. Nest bowls excavated in sandy soil had a greater chance of burrow collapse and chick death than burrows in a guano/shell conglomerate (10% 11/113 in sand, 0% in conglomerate; Table 3) ($TW = 4.3$, df = 1, $P < 0.05$) as opposed to any other cause of death. The probability of burrow collapse (including nonfatal subsidence) after a single day of heavy rain was also related to colony density, regardless of substratum type. Burrows in high-density colonies were more likely to suffer collapse after rain than burrows in low-density colonies (Table 4).

When all causes of nest-related mortality are considered, sand burrows differed from rock nests ($TW = 13.3$, df = 1, $P < 0.001$), primarily because of the risk of burrow collapse ($TW = 6.9$, df = 1, $P < 0.005$). Burrows in conglomerate did not differ from rock nests overall ($TW = 1.5$,

df = 1, $P > 0.2$), but differed in the risk of chick death due to exposure or drowning ($TW = 5.8$, df = 1, $P < 0.05$). This reflects the greater retention of water in nests excavated in a dense substratum.

## DISCUSSION

*Survival.*—Post-hatch Jackass Penguin chicks faced two distinct periods of risk: 0–34 days (64% of losses) and 42–90 days (34% of losses). Wilson (1985) reported a 50% chick mortality before chicks were 15 days old. Randall et al. (1986) found small chicks (<20 days) were most at risk of hypothermia. Jackass Penguin chicks probably attain full thermoregulatory capacity at approximately 400 g body mass (Erasmus and Smith 1974), consequently chicks that weigh <400 g (ca. 10 days old, Williams and Cooper 1984) are most at risk in wet and cold conditions. By 2 weeks of age chicks may weigh >600 g (Y. van Heezik and P. J. Seddon unpubl. data) and are presumably less susceptible to fatal cooling.

Burrow collapse may indirectly cause chick deaths due to crushing by the attending adult when chicks are still closely brooded, or directly through smothering. Collapses may kill chicks up to 30 days, although chicks older than approximately 3 weeks could extricate themselves from all but a total burrow cave-in.

Chicks are vulnerable to predation from the time they hatch until they are ca. 30 days old. They are then presumably able to defend themselves. Until chicks are ca. 2 weeks old predation is probably mainly by Kelp Gulls. Older
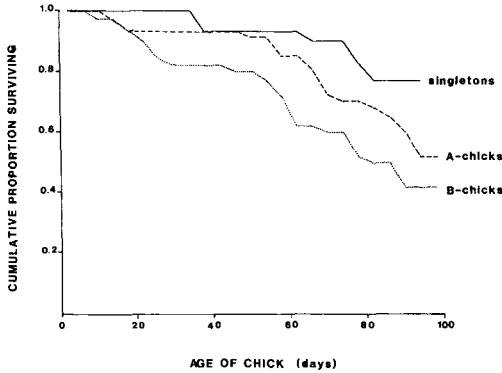
Fig. 2. Estimates of the survivor functions of A-, B-, and single Jackass Penguin chicks in control nests, showing the cumulative proportion of chicks that survive to the beginning of each 4-day interval. Only mortality due to starvation is considered.

chicks may also succumb to gulls and opportunistic predators such as the Sacred Ibis (Cooper 1974). Most predation of chicks between 14 and 30 days is probably due to feral cats (Cooper 1974), which can enter nests sites inaccessible to gulls. Partial burrow collapses that erode burrow entrances and expose young broods may facilitate predation.

Chicks may succumb to starvation from 4 days post-hatch onwards, with an increased probability of starvation after 50 days. Davis and McCaffrey (1986) found Adélie Penguin (*Pygoscelis adeliae*) chicks were at the greatest risk of starvation at 6–8 days old, and suggested that the failure of a parent to return to the nest was the primary cause. The increased likelihood of starvation of Jackass Penguin chicks >50 days
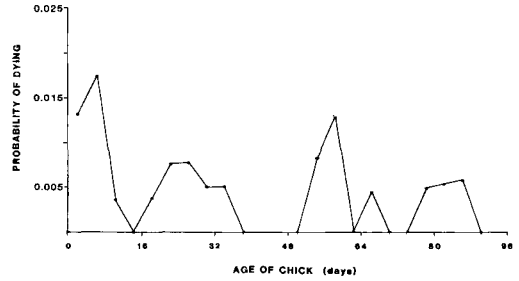


Fig. 3. Hazard functions for 78 Jackass Penguin chicks in experimental broods that contain similarly sized siblings, showing the probability that chicks that survive to the beginning of each 4-day interval will die within that interval. All causes of mortality are considered.

coincides with the chicks' peak food demands (40–70 days; Cooper 1977). The availability of food is influenced by intermittent environmental anomalies (Duffy et al. 1984). Fluctuations in food quality and quantity are thought to be responsible for variation in growth rates between years (Wilson 1985). The continued presence of adults at the nest, and fluctuating chick weights suggest that it was unpredictability of the food supply available to adults, rather than desertion by parents, that caused starvation. Evidence strongly suggests that in the season of our study the availability of prey fish was low (Seddon and van Heezik in press).

*Brood size and hatching order.*—Considering the lack of difference in survival between one- and two-chick broods, we suggest that it is not the number of chicks in the nest so much as competition between siblings that results in un-

TABLE 2. Mortality and survival of A-, B-, and single chicks in control and experimental groups of Jackass Penguins.

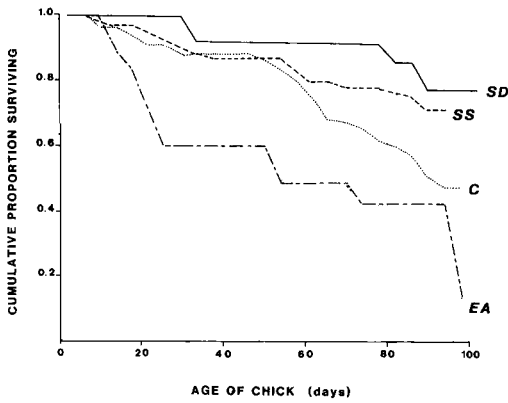| | Control (n [%]) | Experimental | | Single (n [%]) |
|---|---|---|---|---|
| | | Different-size (n [%]) | Extended asynchrony (n [%]) | |
| A-chicks | | | | |
| Total hatched | 53 | 8 | 10 | 33 |
| Died of starvation | 16 (30) | 1 (13) | 3 (30) | 4 (12) |
| Lost to other causes | 12 (23) | 2 (25) | 1 (10) | 15 (46) |
| Fledged | 25 (47) | 5 (62) | 6 (60) | 14 (42) |
| B-chicks | | | | |
| Total hatched | 53 | 8 | 10 | — |
| Died of starvation | 19 (36) | 2 (25) | 8 (80) | — |
| Lost to other causes | 21 (40) | 0 (0) | 2 (20) | — |
| Fledged | 13 (24) | 6 (75) | 0 (0) | — |

Fig. 4.   Estimates of the survivor functions of Jackass Penguin chicks in control and experimental groups, showing the cumulative proportion of chicks that survive to the beginning of each 4-day interval. Only mortality due to starvation is considered. Abbreviations: SD = differently sized siblings; SS = similarly sized siblings; C = control two-chick nests; and EA = extended asynchronous siblings.

equal probabilities of starvation. The difference in survival between single chicks and B-chicks, and between B-chicks and A-chicks in control nests suffering losses due to starvation only, points to the inability of the smaller second-hatched chicks to compete equally with their larger siblings.

Under the brood-reduction hypothesis (Lack 1947, 1954, 1968), hatching asynchrony and competitive asymmetries between siblings are responses to an environment with unpredictable food resources. As a result, the later-hatched sibling starves when food is scarce. One prediction from this hypothesis is that in years of poor food supply, survival until fledging should

TABLE 4.   Effect of nesting density on the incidence of burrow collapse, in sand and shell/guano conglomerate (SGC), following heavy rain. Levels of significance * = $P < 0.05$; *** = $P < 0.001$. High density = mean inter-nest distance ca. 1 m; low density = mean inter-nest distance ca. 3 m.

|  | Colony type | | |
|---|---|---|---|
|  | High density | Low density |  |
| Nest sites | ($n$ [%]) | ($n$ [%]) | $P^a$ |
| Sand burrows |  |  | * |
| Intact | 17 (61) | 48 (83) |  |
| Collapsed | 11 (39) | 10 (17) |  |
| Total | 28 (100) | 58 (100) |  |
| SGC burrows |  |  | *** |
| Intact | 20 (56) | 44 (94) |  |
| Collapsed | 16 (44) | 3 (6) |  |
| Total | 36 (100) | 47 (100) |  |

[a] Chi-square test, high density vs. low density, df = 1.

be higher in asynchronous than in synchronous broods. Although survival analysis is not able to test this directly, the greater probability of survival of similarly sized chicks compared with normal aysnchronous chicks implies that Lack's hypothesis may not be an adequate explanation for Jackass Penguin hatch asynchrony. Starvation of control chicks was greatest between 60 and 90 days of age, when chick demands for food are high. In control nests, competitive asymmetries between siblings result in unequal food distribution, and an increased likelihood of B-chick starvation. Davis and McCaffrey (1989) found that food allocation to Adélie Penguin siblings was influenced primarily by sibling competition. The larger A-chick had the advantage. In nests of similarly sized chicks competition for food was intense and siblings

TABLE 3.   Comparison of causes of mortality of Jackass Penguin chicks in nests under rocks, in the open, and in burrows excavated in either sand (sand-B) or in shell/guano conglomerate (SGCB). Values in parentheses are percentages of total chick numbers.

|  | Burrow type | | | | |
|---|---|---|---|---|---|
|  | Rock | Open | All burrows | Sand-B | SGCB |
| No. of chicks | 60 | 15 | 153 | 113 | 40 |
| No. of losses |  |  |  |  |  |
| Collapse | 0 (0) | 0 (0) | 11 (7) | 11 (10) | 0 (0) |
| Exposure | 0 (0) | 2 (13) | 9 (6) | 5 (4) | 4 (10) |
| Accident | 4 (6) | 0 (0) | 18 (12) | 15 (13) | 3 (8) |
| Predation | 1 (2) | 0 (0) | 9 (6) | 9 (8) | 0 (0) |
| Disappearance | 1 (2) | 4 (27) | 2 (1) | 2 (2) | 0 (0) |
| Total[a] | 6 (10) | 6 (40) | 49 (32) | 42 (37) | 7 (18) |

[a] Excluding starvation.

appeared to be matched equally. This may have equalized distribution of food between siblings, and produced no differential mortality and therefore greater probability of survival in the face of moderate food shortages. It also resulted in retarded growth relative to control A-chicks (van Heezik and Seddon in prep.). Similarly sized chicks were fed less efficiently than control chicks, and the improved efficiency of feeding in control nests is expressed as shorter time taken to fledge and higher chick body weights, rather than differences in final overall survival (Seddon and van Heezik in press).

Differences in the probability of survival between chicks in experimental broods with asynchrony reduced from the normal and the naturally occurring asynchronous control chicks may also have been influenced by different rates of food delivery. On several occasions, after B-chick starvation at control nests, we observed an apparent decrease in provisioning by parents of the surviving A-chick, which resulted in the eventual death of the A-chick. It has been suggested that avian parents do not deliver food at a fixed optimal rate, but at a rate determined by the overall intensity of chick begging (Bengtsson and Ryden 1981). The smaller mass differences between Jackass Penguin siblings the greater the competition, and therefore the greater the intensity of begging vocalizations and physical contact with the adult during feeding. Some theoretical models of the evolution of begging behavior assume that parents respond to the aggregate amount of begging at the nest (Stamps et al. 1989). Thus relatively greater stimulus to deliver food may be found at Jackass Penguin nests that contain equal-sized siblings. The loss of a B-chick in a control nest would decrease the total amount of begging and may lower feeding rates. The foraging rate of gulls has been shown to be regulated by the brood's cumulative calling rate, which increased with brood size (Henderson 1975). At present nothing is known of the relationship between parental feeding rates and chick begging in the Jackass Penguin.

Nest site.—We found chick losses to be lowest in rock nests, intermediate in burrows, and highest in open nests. The weaker structure of burrows in sand make them prone to collapse (LaCock 1988), while the poor drainage properties of burrows in denser shell/guano conglomerate increase the probability of flooding. Burrow nesting is thought to be a response to

high ambient temperatures and intense solar insolation (Frost et al. 1976b, Randall 1983). Jackass Penguins are believed to have traditionally excavated burrows in the thick guano cap that once covered their breeding islands; commercial removal of guano has affected breeding success by forcing the birds to nest on the surface (Frost et al. 1976a), or to burrow into alternative substrata.

The incidence of burrow collapse is greater in high-density aggregations of nests than in areas where nests are well spaced. It is likely that the digging of new burrows, the re-excavation of old ones, and the burrowing by both adults and chicks throughout breeding, combines with the heavy traffic of birds over and around burrows to weaken substantially the soil in closely-packed colonies.

Exposed nests consistently suffer the highest levels of nest failure (Frost et al. 1976a, Cooper 1980, this study). Chicks in open nests risk dying of hypothermia, particularly in wet weather with strong winds, while the easy accessibility of open nests increases chick losses due to gull and ibis predation.

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