

## OFFSPRING REDUCTION IN MACARONI AND ROCKHOPPER PENGUINS

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**ABSTRACT.**—Mortality of Macaroni Penguin (*Eudyptes chrysolophus*) and Rockhopper Penguin [*E. chrysolome (crestatus)*] eggs and chicks was investigated at Marion Island. Two eggs were laid at each nest, but no pair reared more than one chick. Egg mortality exceeded chick mortality in both species. Both eggs hatched at 6% of Rockhopper Penguin nests and at no Macaroni Penguin nests. When both eggs hatched, one chick died of starvation within 12 days. Chicks were successfully reared from 43% and 34% of all eggs laid by Macaroni and Rockhopper penguins, respectively. Egg mortality was greater and occurred earlier, and chick mortality was lower, in Macaroni than in Rockhopper penguins.

Offspring reduction was closely related to egg dimorphism and differential egg mortality. In both species the first laid (A) egg was markedly lighter than the second (B) egg. Mortality of A-eggs was 99.7 and 88% and of B-eggs 44 and 32% in Macaroni and Rockhopper penguins, respectively. Chicks were raised successfully from 3% of all A-eggs laid by Rockhopper Penguins. No A-egg chicks were reared by Macaroni Penguins. The B-eggs, a better investment, were treated preferentially, and the smaller A-eggs were often disregarded. The A-egg functions as an insurance against the loss or failure to hatch of the B-egg in most Rockhopper Penguin clutches but serves no obvious function in the majority of Macaroni Penguin clutches. *Received 23 July 1979, accepted 26 March 1980.*

BIRDS of many species may lay more eggs per clutch than the number of chicks that they are able to raise to independence, and it is generally assumed that the necessary reduction in the number of offspring occurs through brood reduction—the differential mortality of chicks in relation to their position in the hatching sequence (e.g. Ricklefs 1965, Lack 1966, O'Connor 1978, Howe 1978). *Eudyptes* penguins lay a standard clutch of two eggs, in which the first laid (A) egg is markedly smaller than the second laid (B) egg (Gwynn 1953), but rear only one chick per clutch (Warham 1975). Accounts of mortality in Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins [*E. chrysolome (crestatus)*] indicate that the adjustment in offspring numbers occurs primarily through differential egg mortality—the loss or failure of eggs in relation to their position in the laying sequence (Gwynn 1953, Warham 1975).

No account of egg and of chick mortality in either the Macaroni or Rockhopper penguin has been comprehensive. Reports of egg mortality either do not state the number of nests at which both eggs were lost (Gwynn 1953) or, in cases involving the loss of only one egg, do not indicate whether it was the A- or B-egg that was lost (Warham 1963, Duroselle and Tollu 1977). There has been no quantitative assessment of chick mortality. Warham (1963, 1971) reported that in both species both eggs may be hatched at some nests but that the proportion of nests at which this occurs and the period of sibling coexistence were not known.

The mortality of eggs and chicks of Macaroni and Rockhopper penguins was investigated at Marion Island (46°45'S, 37°45'E) in the austral summers of 1974–75 and 1976–77. Particular attention was paid to differences in the pattern of mortality between the two species and differences in the degree and timing of the mortality of A- and B-eggs and ensuing chicks.

## METHODS

The duration of phases in the breeding cycle is similar in the two species. At individual nests, the egg period lasts 40 and 39 days in the Macaroni and Rockhopper penguins, respectively, and in both species the chick-rearing period lasts 70–71 days.

Mortality was assessed during five phases: (1) the laying phase, the 4-day interval between the laying of the A- and B-eggs; (2) the incubation phase, from the laying of the B-egg until the first of the eggs hatches; (3) the hatching phase, from the hatching of the first egg until the second egg hatches or clearly fails; (4) the guard phase, the 3 weeks immediately following hatching during which the male parent remains at the nest guarding the chick; and (5) the postguard phase, from the end of the guard phase until the chick leaves the colony.

Mortality was assessed at several colonies with populations ranging from tens to hundreds of pairs. Study populations all bred on broken, sloping lava terrain. This restricted the effect of human disturbance but made it impossible to analyze the effect of location (edge to center) on mortality. Mortality in the laying phase was assessed in 1976, when the contents of individually numbered nests were monitored daily. Most birds permitted nest inspection and handling of the eggs without leaving the nest site. My movement through colonies was slow and careful. If birds left their egg(s), I remained close by to deter predators until the parents returned. There was no appreciable difference in the reaction of birds in the two species to human disturbance. When there was any doubt whether my activity had affected egg loss, the record for that nest was discarded. Males of both species return to their nest site in the latter part of the egg period and remain at the nest irrespective of its contents until some time after all the chicks in the colony have hatched. Egg mortality during incubation and hatching phases was assessed by inspecting the contents of individually numbered nests a few days before hatching was due and then monitoring their contents daily until after hatching was completed.

Chicks were weighed within 24 h of hatching and daily thereafter until they were fed (indicated by a marked increase in chick weight compared with egg weight at the end of incubation), until brood reduction had occurred, or until the chick died or became independent and went to sea. During the guard phase, chicks remained at the nest, and any missing from the nest were assumed to have been killed and removed by predators. Chicks were given numbered plastic flipper tags when about 15 days old. Some Rockhopper Penguin chicks moved into inaccessible cavities at the end of the guard phase and could no longer be monitored. The number of singly reared A-egg chicks was increased by removing some B-eggs from nests that had retained both eggs through the incubation period.

## RESULTS

*Egg mortality.*—Egg mortality was substantial in both species, and 72% of all Macaroni Penguin eggs and 60% of all Rockhopper Penguin eggs were lost or failed to hatch. The pattern of egg mortality in the two species differed in several ways (Table 1). Total nest failure through the loss of both eggs was greater in Macaroni than in Rockhopper Penguins. Egg mortality occurred earlier in Macaroni Penguins, and at no Macaroni Penguin nests were both eggs retained until the end of the incubation phase. Both eggs remained at 30% of all Rockhopper Penguin nests, but, because of mortality in the hatching phase, both eggs hatched at only 6% of all nests (Table 1).

Mortality of A-eggs was 99.7 and 88%, and of B-eggs it was 44 and 32% in Macaroni and Rockhopper penguins, respectively (Table 1). Loss of the A-egg during the laying phase amounted to almost 54% in the Macaroni Penguin but was less than 2% in the Rockhopper Penguin. Macaroni Penguins also lost more single eggs than Rockhopper Penguins during the incubation phase. Mortality in the hatching phase was confined to Rockhopper Penguins and was largely due to the loss of A-eggs from the nest after the B-egg had hatched. A-eggs found beside Rockhopper Penguin nests during this phase almost all contained well developed embryos and some of the eggs were piped.

TABLE 1. Mortality of Macaroni and Rockhopper penguin eggs at Marion Island.

|                                       | Macaroni Penguin |          |                   | Rockhopper Penguin |          |         |
|---------------------------------------|------------------|----------|-------------------|--------------------|----------|---------|
|                                       | A-egg %          | <i>n</i> | B-egg %           | A-egg %            | <i>n</i> | B-egg % |
| Laying phase                          |                  |          |                   |                    |          |         |
| Number of nests sampled               |                  | 24       |                   |                    | 53       |         |
| Loss of A-eggs before B-eggs laid     | 53.6             |          | —                 | 1.9                |          | —       |
| Combined laying and incubation phases |                  |          |                   |                    |          |         |
| Number of nests sampled               |                  | 300      |                   |                    | 258      |         |
| Loss of both eggs                     | 44.0             |          | 44.0 <sup>a</sup> | 26.0               |          | 26.0    |
| Loss of single eggs                   | 55.7             |          | 0.3               | 39.1               |          | 4.7     |
| Both eggs retained until one hatched  | 0                |          | 0                 | 30.2               |          | 30.3    |
| Hatching phase                        |                  |          |                   |                    |          |         |
| No. nests (with 2 eggs) sampled       |                  | 0        |                   |                    | 35       |         |
| Loss of single eggs                   | —                |          | —                 | 77.0               |          | 3.0     |
| Both eggs lost                        | —                |          | —                 | 0                  |          | 0       |
| Both eggs hatched                     | —                |          | —                 | 20.0               |          | 20.0    |
| Total egg mortality                   | 99.7             |          | 44.3              | 88.0               |          | 32.0    |
| % all eggs lost or failed             |                  | 72       |                   |                    | 60       |         |

<sup>a</sup> Includes five B-eggs that were addled and one where the chick died in the egg. The proportion of addling in Rockhopper Penguins was not ascertained.

Most of the eggs lost simply disappeared, either stolen directly from the nest by Lesser Sheathbills (*Chionis minor*), Skuas (*Catharacta skua*), or Kelp Gulls (*Larus dominicanus*) or dislodged from the nest by the parents and then taken by scavengers. No replacement eggs are laid (Gwynn 1953, pers. obs.).

**Brood reduction.**—No Macaroni Penguins hatched both eggs. At 18 Rockhopper Penguin nests where two chicks hatched, only one of the brood survived. Coexistence of the siblings ranged from 2 to 12 days. At 17 nests where an A- and a B-egg hatched, 16 B-egg chicks and one A-egg chick survived. In one nest two A-eggs hatched (the result of the capture of a dislodged A-egg after the B-egg was lost). At this nest the first chick to hatch survived, and the second chick died 12 days after hatching.

Three principal factors affected the length of time two chicks coexisted: (1) the degree of hatching asynchrony; (2) the difference in size and weight of the chicks when the second chick hatched; and (3) the time elapsed before the chicks received their first meal. Typically, the B-egg hatched first and the B-chick was fed before the A-chick hatched. The A-chick was not usually fed and died from starvation within 4 days. The period of sibling coexistence was increased when both chicks hatched on the same day. One A-chick hatched, and was fed, before the B-chick hatched. Though equal in weight to the B-chick, it was smaller in size and was dominated by the B-chick in competition for food and soon died. The only A-chick that outlived its B-sibling was at a nest where the chicks were not fed until the B-chick was at least 132 h old. The B-chick was by that time too weak to compete with the later-hatched A-chick and died of starvation.

**Chick mortality.**—The overall chick mortality was 22% in Macaroni and 61% in Rockhopper Penguins (Table 2). The principal differences were the absence of brood reduction in Macaroni Penguins and the markedly greater mortality of Rockhopper Penguin chicks during the postguard phase.

TABLE 2. Percentages of chick mortality and hatching and overall breeding success of Macaroni and Rockhopper penguins at Marion Island. Sample sizes are given in parentheses.

| Species and chick type        | Hatching success <sup>a</sup> | Chick mortality                      |                             |                    | Breeding success <sup>d</sup> |
|-------------------------------|-------------------------------|--------------------------------------|-----------------------------|--------------------|-------------------------------|
|                               |                               | Through brood reduction <sup>b</sup> | In guard phase <sup>c</sup> | In postguard phase |                               |
| Rockhopper Penguin            |                               |                                      |                             |                    |                               |
| A-egg chicks <sup>a</sup>     | 12.0                          | 94.0 (17)                            | 8.0 (26)                    | 50.0 (18)          | 3.2                           |
| B-egg chicks                  | 68.0                          | 6.0 (17)                             | 18.0 (62)                   | 43.0 (40)          | 31.7                          |
| Macaroni Penguin <sup>e</sup> |                               |                                      |                             |                    |                               |
| B-egg chicks                  | 55.7                          | — —                                  | 14.9 (67)                   | 8.8 (57)           | 43.2                          |

<sup>a</sup> Success per 100 eggs of each type.

<sup>b</sup> Brood reduction affected 50% of Rockhopper A-chicks, 6% of B-chicks, and no Macaroni Penguin chicks.

<sup>c</sup> Mortality in the guard phase excludes mortality through brood reduction.

<sup>d</sup> Two broods of two A-chicks have been treated as cases of single A-chick survival.

<sup>e</sup> Only one Macaroni Penguin A-egg chick hatched. The chick died within 48 h.

Chicks from A- and B-eggs of both species were usually viable and could be successfully reared by their parents, although in natural circumstances no Macaroni Penguins reared an A-egg chick. The great majority of chicks that survived until independent were, however, from B-eggs (Table 2). The mortality rate of Rockhopper Penguin A-chicks hatched and raised singly was 46%, the same as that of B-chicks.

The cause of death was known in few cases. Most chicks simply disappeared, the majority probably killed and removed by Subantarctic Skuas. Chick mortality in the postguard phase was greater in Rockhopper Penguins because, being smaller than Macaroni Penguin chicks, they were preyed upon by skuas until they were older.

*Breeding success.*—The number of chicks reared to independence per pair was 0.43 in the Macaroni Penguin and 0.35 in the Rockhopper Penguin (Table 2). Differential mortality was such that only 3% of all Rockhopper Penguin A-eggs, and none of the Macaroni Penguin A-eggs, gave rise to successfully reared chicks.

## DISCUSSION

The results confirm that in the Macaroni and Rockhopper penguins offspring reduction occurs primarily through differential mortality of the eggs and that only one chick may be reared from each clutch.

Differential egg mortality is an expression of parental investment (*sensu* Trivers 1972). The B-eggs of both species contain more provisions than A-eggs and give rise to larger hatchlings, which complete growth earlier and are heavier at independence than those from A-eggs (Williams MS). The B-eggs, therefore, form a bigger and better investment than the A-eggs. In both species the B-egg is treated preferentially, and the A-egg is often disregarded (Warham 1963, Downes 1955, Burger and Williams 1979). Tinbergen (1951) has demonstrated a similar preference for relatively large eggs in other bird species.

The two prime causes of differential egg mortality are displacement from the nest and theft by a predator. Displaced eggs are normally ignored if the B-egg remains in the nest (Downes 1955). Egg mortality is greatest during incubation when the

positioning of the egg with respect to the broodpatch appears to be critical. Penguins possess a single elongated broodpatch against which the eggs are positioned one in front of the other. The posterior position, in which the egg is tucked between the adult's feet, is the safest. The egg in the anterior position is more often exposed and more accessible to predators and is also more readily dislodged from the nest than is the posterior egg. The B-egg occupies the safest posterior position significantly more often than the A-egg in the Rockhopper Penguin (Burger and Williams 1979) and probably also in the Macaroni Penguin.

Differential egg mortality is more pronounced in the Macaroni Penguin than in the Rockhopper Penguin. The difference in egg mortality may be attributed partially to the greater safety of eggs in Rockhopper Penguin nests. Macaroni Penguins normally incubate in a more erect posture, which provides less security for the eggs, than the posture used most frequently by Rockhopper Penguins. Rockhopper Penguins prefer to nest against natural features such as rocks or grass tussocks. At such sites materials are usually available for nest building, and disturbance, which can lead to egg loss through displacement, is limited. Macaroni Penguins breed at high density on open areas where disturbance is more frequent and may come from any direction and where fewer materials are available for nest building. The difference in egg security resulting from these dissimilarities may be compounded by the effect of egg dimorphism. Preferential treatment of the B-egg and disregard for the A-egg should be more developed in the Macaroni Penguin, in which egg dimorphism is more marked (Gwynn 1953, Williams MS), than in the Rockhopper Penguin. The great loss of A-eggs by Macaroni Penguins during the laying phase may also be due to the eggs being dislodged from the nest during nest scraping, which precedes the laying of the B-egg and which is more pronounced in this species than in the Rockhopper Penguin (Williams 1977).

*Eudyptes* penguins are not the only birds that, though laying a two-egg clutch, invariably raise only a single chick. A similar situation occurs in some species of boobies (Nelson 1978), cranes (Miller 1973), and raptors (Newton 1978). Many other bird species, including most other penguins, lay two-egg clutches but may raise one or two chicks from each clutch. Except for Macaroni and Rockhopper penguins (and probably all other *Eudyptes* penguins), birds with two-egg clutches normally retain both eggs in the nest until one or both hatch. Offspring reduction then occurs through desertion of one egg or, if both eggs hatch, through the death of the weaker chick by starvation or sibling aggression. Thus offspring reduction takes place only after the "surplus" egg has already functioned as an insurance against both the loss and the failure to hatch of the "preferred" egg. An insurance function for *Eudyptes* A-eggs has been claimed by Lack (1968) and Howe (1976), and this is the case for a minority of Rockhopper Penguins, for at 35% of the nests the A-egg is retained until the end of the incubation phase (Table 1). Egg mortality in Macaroni and Rockhopper penguins is greatest during the first half of the incubation phase (Gwynn 1955, Warham 1963, pers. obs.), and the A-egg may still function as an insurance against B-egg loss if it is retained through this stage. This seems to be the case in about 60% of Rockhopper Penguin nests but at very few Macaroni Penguin nests (Downes et al. 1959, pers. obs.). Thus, at our current level of appreciation, the A-egg serves no obvious function in the clutches of the great majority of Macaroni Penguins and in a substantial minority of Rockhopper Penguins.

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