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Consequences of Nest Desertion and Inattendance for Magellanic Penguin Hatching Success

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Advantages of shared parental care during incubation are that eggs are attended at all times, protected against predators, and incubated at the correct temperature (White and Kiney 1974). However, egg neglect and desertion by parents are frequent in many bird species (Boersma 1982, Yorio and Boersma in prep.). Nest desertion increases egg losses for several seabird species (Boersma 1976, Davis 1982, Johnstone and Davis 1990), and has been suggested as the main cause of decreased hatching success in the Magellanic Penguin (*Spheniscus magellanicus;* Scolaro 1984, 1990).

In Magellanic Penguins, eggs abandoned by an incubating bird may be left unattended for several days until the mate returns to resume incubation. When left unattended, eggs are exposed to factors that affect their probability of survival, such as extreme temperatures and predation. Temporary desertion may result in decreased likelihood of hatching if eggs are exposed to suboptimal temperatures (Hunt 1972, Hunter et al. 1976, Boersma and Wheelright 1979, Phillips 1987). At Punta Tombo, in Argentina, penguin eggs and chicks are mainly preyed upon by Kelp Gulls (*Larus dominicanus*), Southern Skuas (*Catharacta* [*skua*] *antarctica*), hairy armadillos (*Chaetophractus villosus*), and grey foxes (*Dusicyon griseus*). Other potential predators are Patagonian ferrets (*Lyncodon magellanicus*), Patagonian skunks (*Conepatus humboldti*), and Dolphin Gulls (*Larus scoresbii;* Conway 1971, Rodriguez 1983, Scolaro 1985). The goals of our study were to: (1) determine and quantify the causes of egg loss; (2) evaluate the effects of nest desertion on hatching success; and (3) assess the importance of nest desertion as a cause of predation and embryo mortality.

Punta Tombo Provincial Reserve, Chubut, Argentina (44°02'S, 65°11'W), has a diverse seabird colony and the largest continental colony of Magellanic Penguins (Boswall and McIver 1975, Boersma et al. 1990). Magellanic Penguins have a seasonal breeding schedule, arriving at the colony to breed in late August or early September. They lay two eggs in early October, hatch chicks in November, fledge chicks in late January and February, and molt before they migrate north in March or early April. Both sexes defend the nest site, incubate eggs and feed young. Males and females take turns incubating eggs, which hatch approximately 40 days after being laid (Boersma et al. 1990).

Over 100 nests were marked in an area (site 1) of approximately 180 × 70 m, and studied during each breeding season from 1983 to 1989. At each nest, adults were banded with numbered stainless-steel flipper bands. Nests were checked daily from early September to January to monitor adult presence and nest contents. Thus, laying and hatching dates, as well as egg losses, were recorded daily.

Eggs were marked with a number corresponding to their laying order and nest number. At each visit we recorded if the eggs were being incubated, left alone, or missing. Egg loss was categorized by cause: (1) predation; (2) desertion; (3) addled; (4) broken; (5) died during hatching; or (6) broken by investigators. For a more detailed analysis, the predation category was further subdivided into three categories: (a) preyed on by an avian predator (if broken egg shells were away from the nest or if eggs had a hole characteristic of avian predators); (b) preyed on by hairy armadillos (if signs of digging found in or around nest, or if egg shells were smashed and in small fragments); and (c) preyed on by an unknown predator (if eggs disappeared from nest and no signs to identify the predator were found). The laying sequence markings on the eggs allowed egg shells found outside and away from nests to be identified.

Each year of the study, samples of eggs that had not hatched 10 to 15 days after the expected hatching date were opened to determine if they showed signs of development. Addled eggs were subdivided into two categories: (a) those with embryos that died after some visible development; and (b) those with no visible embryo development. The latter category included eggs that were infertile, as well as those where the embryo died at an early stage.

In 1990, as a control for egg loss due to researcher disturbance during incubation, we checked 49 nests every four days in an area similar to site 1 in nest density and habitat (100 m from this study area). Neither birds nor eggs were handled, but the presence or absence of adults and eggs were recorded.

Eggs found unattended for only one check and where the same parent was attending the nest on the previous and following day were considered neglected. If eggs were found unattended and adults were not seen at the nest during at least two consecutive nest checks, the nest was considered deserted.

From 1983 to 1989, 306 eggs were lost from 1,346 eggs laid at 692 nests in the site 1 area (Table 1). The percent of eggs lost varied among years, ranging from 13.28% ($n = 143$) in 1983 to 37.00% ($n = 100$) in 1984. Average egg loss for the seven years of the study was

TABLE 1. Causes of Magellanic Penguin egg loss over a seven-year period at Punta Tombo, Argentina. Percents of total eggs lost are shown for nests at site 1.

Year	Eggs laid	Predation	Desertion	Addled	Broken	Died	Human	Total
1983	143	4.19	2.80	2.10	3.50	—	0.70	13.28
1984	100	11.00	13.00	3.00	7.00	1.00	2.00	37.00
1985	226	4.42	5.75	8.85	4.42	0.44	—	23.89
1986	197	5.08	5.08	2.03	2.54	—	—	14.72
1987	236	4.24	4.24	6.35	3.81	0.42	0.42	19.49
1988	209	8.13	5.26	2.87	5.26	—	0.48	22.01
1989	235	17.87	1.70	9.79	2.55	—	—	31.91

23.2 ± SD of 8.7% ($n = 7$). Egg losses due to predation for the seven years averaged 7.85 ± 5.10% ($n = 7$). First and second eggs from nests with two-egg clutches ($n = 187$) were equally likely to be lost ($X^2 = 0.088$, df = 1, $P > 0.05$).

During 1990, egg losses at site 1 were similar to those at the control area ($X^2 = 0.48$, df = 1, $P > 0.05$). The percentage of eggs lost at site 1 was 14.6% of all eggs laid, while the percentage for the control area was 17.9%.

Eggs from 78 nests were lost to predators during the seven breeding seasons. In 25 of the nests preyed upon when the adult was in attendance, the predator species was identified. Armadillos took eggs from 18 nests and avian predators took eggs from 7. The presence of potential avian predators in the area shed light on which species are responsible for most of the predation. Kelp Gulls were commonly seen searching for food in the study area, either flying over or standing near nests. Several times they were observed stealing eggs from nests with adults in attendance or eating egg remains in neighboring areas. Southern Skuas were never seen searching for food in the study area, although they occasionally took food from Kelp Gulls. Even though other authors have suggested that Dolphin Gulls are egg predators, we never observed them searching for food in the study area during the penguin incubation period. In areas where Dolphin Gulls frequent, we did not observe them take any eggs, although they commonly scavenge eggs taken by other predators.

TABLE 2. Desertion losses for Magellanic Penguins at site 1 from 1983 to 1989. Number of nests deserted and percentage of eggs lost.

			Eggs	
Year	No. nests	No. nests deserted	No. laid	Percent deserted (no.)
1983	73	2	143	2.80 (4)
1984	53	8	100	13.00 (13)
1985	114	7	226	5.75 (13)
1986	100	7	197	5.08 (10)
1987	124	6	236	4.24 (10)
1988	110	7	209	5.26 (11)
1989	118	2	235	1.70 (4)

Addled eggs accounted for 5.0 ± 3.3% ($n = 7$) of the egg losses. Of 61 eggs that failed to hatch but appeared to be intact, 34 (55.74%) had some development and 27 (44.26%) had no signs of development.

Of 692 nests followed, 39 nests with 65 eggs were deserted. Average percentage of nests where deserted eggs were eventually taken by predators was 6.3 ± 4.4% ($n = 7$). The percentage of eggs lost after being deserted varied among years, with an average loss of 5.4 ± 3.6% ($n = 7$) of all eggs laid (Table 2).

Of the total number of eggs lost to predators, 25 (14.62%) disappeared from nests where the adult was absent for the first time. Due to our operational definition of nest desertion, these eggs were categorized as lost while the adult was still present at the nest. However, some of these eggs might have actually been lost after being deserted and, thus, a maximum of 15% of the eggs in all years could have been incorrectly categorized.

Predators took eggs from 83 attended and unattended nests with two-egg clutches and, in 54 (65%) of these, the complete clutch was lost. Deserted nests were more likely to lose the complete clutch to predation than nests where one of the parents was attending the eggs ($X^2 = 7.40$, df = 1, $P = 0.006$).

Of 65 eggs that were deserted, 58% were taken by predators while the egg was exposed. For the remaining 42%, one of the parents returned to the nest before the eggs disappeared, and 13.39% hatched. Eight additional eggs from six nests were neglected for less than one day. Eggs that were either deserted or neglected at least once were more likely to be lost to predators than eggs that were never left unattended ($X^2 = 197.84$, df = 1, $P < 0.0001$). Of the nests where eggs were preyed on when left unattended and the predator was identified ($n = 19$), 12 (63.2%) were preyed on by Kelp Gulls and 7 (36.8%) by hairy armadillos. Hairy armadillos were more likely to take eggs from attended nests and Kelp Gulls from unattended nests ($X^2 = 5.44$, $P < 0.02$). We observed hairy armadillos enter occupied penguin burrows without apparent injury. Of the nests identified as lost to hairy armadillos during the seven years, 61% ($n = 18$) were lost during 1989.

Nine of 40 eggs deserted within the average length of the incubation period and not eaten were addled. Deserted eggs that did not hatch were exposed for a significantly longer time than deserted eggs that hatched ($\bar{x} = 6.33 \pm 4.5$ days, range = 1-16, $n = 9$ vs. $\bar{x} = 2.73 \pm 2.0$ days, range = 1-6, $n = 15$; Mann-Whitney $U = 28$, $P = 0.015$). Eggs were more likely to be addled if they were unattended than if they were always attended ($X^2 = 21.08$, df = 1, $P < 0.001$), showing that periods of neglect reduced hatching success. Thus, desertion may have resulted in embryo mortality in as many as 9 (12.16%) of the 74 addled eggs.

Nest desertion is an important factor affecting hatching success in many seabird species, causing as many as one-third of the eggs to be lost (Fisher 1971, Davis and McCaffrey 1986, Johnstone and Davis 1990). The effect of desertion on hatching success in the Magellanic Penguin is relatively minor, resulting in average loss of less than 6% of the eggs laid. Losses due to desertion were lower than those reported by Scolaro (1984), who found 16% egg loss in a sample of 19 Magellanic Penguin nests at Punta Tombo during the 1980 breeding season. Presumably, the difference between our study and his reflects variability among years.

We probably underestimated desertion egg losses because eggs were not classified as having been deserted unless a bird was absent at two successive nest checks. However, even if all cases where the birds and eggs disappeared between checks were considered desertions, the total number of desertion-caused egg losses increases by less than 2%. Therefore, even using this less restrictive definition, nest desertions accounted for no more than 8% of eggs laid for all years except 1984.

Hatching success was variable among years, and egg losses were lower than those reported by Scolaro (1990) for the 1976-1982 breeding seasons. He estimated an average egg loss for the Punta Tombo colony of 46%. Because of his infrequent checking schedule (every 15 to 20 days), Scolaro (1990) likely overestimated egg loss by assuming some early chick losses as egg losses. Early chick mortality at Punta Tombo is high (Boersma unpubl. data). Consistent with this explanation are the results Scolaro (1984) reported for more closely monitored nests, where egg loss was 27%.

Deserted and neglected eggs were more likely to be lost to predators than attended eggs, showing that egg desertion and neglect increased predation. Moreover, deserted nests were more likely to lose the complete clutch to predators than attended nests. The importance of nest inattendance in allowing predation may be underestimated because our nest checking schedule would not allow us to detect more short absences from the nest.

Hairy armadillo predation can be an important selection agent in some years. This was particularly true in 1989, the year with the highest predation rate. Hairy armadillos can apparently prey on penguin eggs with some degree of impunity, in contrast to Kelp Gulls that more often take unattended eggs. Kelp Gulls accounted for most, if not all, of the avian predation losses.

We found no significant difference in egg losses between our control and study areas. However, disturbance can increase predation and have a negative impact. Kelp Gulls have been reported to take unattended eggs from nests where adults fled from people in both the Magellanic Penguin and Jackass Penguin (*S. demersus*; Boswall 1973, Frost et al. 1976, Gochfeld 1980, Hockey and Hallinan 1981). With proper care and management, the negative impacts of human disturbance which can increase predation can be avoided.

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Showiness, Carotenoids, and Captivity: A Comment on Hill (1992)

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Primarily on the basis of the loss of carotenoid pigmentation in captive House Finches (*Carpodacus mexicanus*) and the partially restorative influence of carotenoid supplements, Hill (1992) recently concluded that plumage color variability in male House Finches in the wild is due to differential access to carotenoid pigments at the time of molt, and not to intrinsic differences in the ability of males to use or display carotenoids. While Hill's interpretation appears logical, in many ways extending the work of Brush and Power (1976), it clashes with an imposing body of work from Germany. A probable consequence is that Hill did not really investigate the source of plumage color variation in wild House Finches, as he claimed, but rather evaluated the ability of various pigment-supplementation regimen to reverse color losses incurred in captivity.

German workers have long been aware of the debilitative effects of captivity on carotenoid pigmentation in several birds, notably carduelines, and actively sought ways to remedy these effects (see Völker 1957, Reuter 1964). Heinroth and Heinroth (1926, from the 1966 reprint) discussed possible causes of fading in captive Red Crossbills (*Loxia curvirostra*) and other birds. They found no support for a shortage of carotenoids or an effect of reduced sunlight and surmised that the weakened body condition of captive birds might be responsible instead. Koch (1939) pursued the problem of fading in carduelines further. Red Crossbills and Linnets (*Carduelis cannabina*) replaced their red feathers with yellow ones even in outdoor enclosures in a near-natural setting with an abundance of food and water (Koch 1939). He also found that no vitamin supplements and hormone preparations could reverse the color loss incurred in captivity, although improvements in plumage brightness were seen with certain treatments (Koch 1939).

Weber (1953, 1961) made supplementary observations, and performed a few controlled experiments

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