

# CAUSES OF NEST DESERTION DURING INCUBATION IN THE MAGELLANIC PENGUIN (*SPHENISCUS MAGELLANICUS*)<sup>1</sup>

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**Abstract.** We quantified the causes and rate of nest desertions in Magellanic Penguins (*Spheniscus magellanicus*) during the egg stage at Punta Tombo, Argentina. Incubating Magellanic Penguins rarely deserted. The average desertion rate during seven years was 11% (SD = 9.2%). Desertions were poorly correlated with the length of the incubation spell and only 25% of the desertion could be accounted for by delayed nest relief. Body condition at the start of the incubation spell appears to be the most important factor in determining desertions. Penguins that deserted were lighter for their body size at the time of egg laying than penguins that did not desert. Desertion was significant and common during the first part of incubation, the time when females are present. Flooded nests were more likely to be deserted than nonflooded nests, but desertions from flooding were few. High temperatures did not increase desertion during incubation, thus it is unlikely that heat stress is an important cause of nest desertion. An individual's body condition appears to be the most important factor in explaining desertion but behavior of the mate and other factors can play a role.

**Key words:** *Magellanic Penguin; nest desertion; female condition; incubation.*

## INTRODUCTION

Nest desertion is a common behavior in many seabird species. Factors that cause desertion include lack of food (Boersma 1976, Nelson 1978, Anderson 1989), delayed nest relief (Davis 1982), extreme weather conditions (Fisher 1971, Beck and Brown 1972, Boersma 1976), ectoparasite infestation (Duffy 1983; King et al. 1977a, 1977b), predation (Emlen et al. 1966, Buckley and Buckley 1972, Shealer and Kress 1991), human disturbance (Anderson and Keith 1980, Yorio and Boersma 1992) and inexperience or age (Jouventin 1975).

Nest desertion can occur when nest relief is delayed, resulting in an unusually long spell for the incubating mate. Significant reduction in the incubating bird's fat reserves as a result of unusually long incubation spells is believed to be the main proximate mechanism causing nest desertion (Davis 1982, 1988; Groscolas 1990). However, significant fat reduction could occur during short fasts if the incubating bird is in poor body condition at the start of an incubation spell. Thus, food conditions could determine the rate of desertion either by delaying the return of the foraging mate or by affecting the breeding condition of the incubating bird.

Nest desertions from delayed nest relief due to food shortage should be more likely in seabird species subject to high variability in food availability, with long incubation spells, and variable body condition. The Magellanic Penguin fits this description; it has incubation spells of one to three weeks and at Punta Tombo, Argentina, its food supply appears to be highly variable, probably accounting for the high yearly variability in reproductive success (Boersma et al. 1990). Scolaro (1984) suggested nest desertion due to the delayed return of a mate is one of the main factors determining hatching success of Magellanic Penguins. We tested this hypothesis and quantified the rate of desertions in Magellanic Penguin reproductive success for 1983-1989.

If timing of nest relief is the main cause of nest desertion (nest relief hypothesis), most egg abandonment should occur when one member of the pair is delayed in its return from the foraging trip. Thus, desertion should be more frequent in birds that incubate for longer than the average spell for that year. If physical condition at the start of incubation is a major factor affecting nest desertions (body condition hypothesis), birds in poor body condition could desert even before the average length of their incubation spell. More importantly, penguins that desert should be in worse body condition at the onset of breeding than those that successfully complete incubation.

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These two hypotheses are not mutually exclusive and often may interact. Both body condition and the length of mate absence are factors that a bird must assess when deciding whether to remain or abandon incubation.

Other factors may also affect the desertion rate of the Magellanic Penguins at Punta Tombo, such as extreme weather and human disturbance. We examined the rate of nest desertions during the egg stage and classified the causes of desertions, assessing the importance of food conditions and incubation patterns. In particular, we examined the importance of the nest relief hypothesis and the body condition hypothesis in explaining desertion discussion of Magellanic Penguins.

## METHODS

### STUDY AREA AND SPECIES

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 MacIver 1975). Magellanic Penguins have a seasonal breeding schedule, arriving at the colony to breed starting in late August and early September (see Boersma et al. 1990). 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. Their prey consists of small fish and squid.

Males arrive on land from a few days to a month earlier than females, and both sexes fast during the settlement and laying period. Males and females take turns incubating eggs, and although the time of their incubation spells is variable, most pairs follow a pattern of two long incubation spells followed by up to eight shorter spells. Females generally take the first spell; males generally leave for their first foraging trip some time between the laying of the first and second eggs. The length of the incubation period averages 40 days.

### STUDY DESIGN

During each breeding season from 1983 to 1989, we marked and studied a sample of from 53–124 nests. At every nest, we banded adults with stainless steel flipper bands. We weighed adults with a 6 kg (50 g increments) spring scale and estimated mass to the nearest 10 g. We measured bill length and depth with dial calipers to the

nearest 0.1 mm, and flipper and foot length (from the bend in the tarsus to the end of the middle toe nail) with a ruler to the nearest 1 mm. We determined sex of adults from these morphological measurements by discriminant analysis. Using birds of known sex, measurements alone correctly sexed 95% of 200 birds (Boersma, unpubl. data).

Nests were checked daily from September to January, and at each visit we recorded which bird was present and the nest contents. We weighed eggs with a spring scale to the nearest 1 g. At each visit, we noted egg status (incubated or left alone) and condition (whether still intact, damaged, or gone).

### DEFINITIONS

Even temporary nest abandonment increases the egg's exposure to predation or temperature extremes. Therefore, we considered a bird to have deserted if eggs were found unattended and adults were not seen at the nest for at least two consecutive days, even if the bird eventually returned to the nest. Some of these eggs did hatch. As our nest checking schedule did not allow us to distinguish if absences of the adult from the nest were less than a day, unattended eggs for less than two days were not considered nest desertions.

A bird's fasting period is considered as time elapsed from when it is first seen at its nest at the start of the breeding season until it departs for its first foraging trip in the case of the male, or until relieved by the male in the case of the female. An incubation spell, except for the first one, is the time a bird remains at the nest from its arrival until relieved by its mate. The first incubation spell (Spell 1) is the total days elapsed from the laying of the second egg until the bird was relieved by its mate. Therefore, each foraging trip, except for the first, is equal to the length of the mate's corresponding incubation spell.

In addition, a second analysis used a more restrictive definition, considering that a penguin took an unusually long spell if it incubated for one standard deviation longer than the average spell length. To determine if females that deserted had been at the nest for an unusually long time and may have depleted their fat reserves, we defined the fasting period as the time from the female's arrival on land before egg laying until she was relieved or deserted.

TABLE 1. Nest desertion of Magellanic penguins at Punta Tombo, Argentina from 1983 to 1989. The number of active nests followed throughout the reproductive season, and the percentage and number (*n*) of those deserted are shown. In a few cases both members of the pair deserted, so that the number of nest desertions is not necessarily equal to the number of deserting individuals.

Year	Total nests	Nest desertion		Deserting individuals
		%	( <i>n</i> )	
1983	73	2.7	(2)	2
1984	53	30.2	(16)	17
1985	114	10.5	(12)	12
1986	100	7.0	(7)	8
1987	124	13.7	(17)	18
1988	110	7.3	(8)	8
1989	118	5.1	(6)	6
Total	692	3-30	(68)	71

#### DATA ANALYSIS

A sample that included birds that deserted and had been measured and weighed near egg laying (*n* = 16) and of birds that did not desert (*n* = 115) were used to assess body condition. A body size index was calculated as the first factor extracted from a principal component analysis on measurements of bill length, bill width, flipper and foot length. To estimate females' mass when they laid their first egg, we subtracted or added the average daily weight loss for the number of days between weighing and egg laying (40 g-53 g see results). If a female was weighed before laying, the mass of the eggs was also subtracted.

Because frequent handling of the birds could increase desertion rates, we used a separate sample of birds to determine daily weight loss during the settlement, laying and incubation periods. Weather records were collected daily within the penguin colony with a maximum-minimum thermometer and a rain gauge.

TABLE 2. Average length of the first two incubation spells (Spell 1 and Spell 2) and the fasting period of females from arrival to nest relief (Fast), for 1983-1989. Females take the first incubation shift and males the second.

Year	Spell 1		Spell 2		Fast of females	
	<i>n</i>	$\bar{x}(\pm 1 \text{ SD})$	<i>n</i>	$\bar{x}(\pm 1 \text{ SD})$	<i>n</i>	$\bar{x}(\pm 1 \text{ SD})$
1983	54	13.3 (3.8)	54	11.1 (5.4)	—	—
1984	24	15.7 (2.7)	25	15.4 (4.4)	11	28.9 (4.8)
1985	69	16.4 (3.2)	63	17.2 (4.3)	20	33.6 (3.4)
1986	58	16.5 (2.4)	76	18.3 (3.7)	55	31.6 (4.1)
1987	81	13.9 (3.7)	81	17.6 (4.5)	61	28.0 (4.9)
1988	21	16.1 (3.4)	—	—	40	30.2 (4.1)
1989	21	16.1 (3.4)	60	17.0 (4.8)	41	33.0 (3.9)

For the analysis on timing of breeding, birds were divided into three categories: peak, early, and late breeders, depending on their laying date relative to the median laying date for each year (Boersma et al. 1990). Egg laying is synchronous, with most eggs laid within a three week period (Boersma et al. 1990). Peak breeders were defined as the pairs that laid eggs within two days of the median laying date. Early breeders were those that laid three or more days before the median laying date, and late breeders those that laid three or more days after the median laying date.

#### RESULTS

Seventy-one individuals from 692 nests deserted their eggs from 1983 to 1989 (Table 1). The average percentage of nests deserted was 11.0% (SD = 9.2, *n* = 7). Seven birds left their eggs unattended for less than one day from two to six times before finally deserting, and fourteen (19.7%) of 71 birds returned to the nest in less than a week after temporarily deserting but had already lost the nest contents. Of the 71 individuals that deserted, 47 (66.2%) were females and 22 (31.0%) were males. Sex was not identified for 2 (3.0%) of the deserting birds.

#### TIMING OF DESERTIONS

Of the 71 desertions, 3 (4.2%) occurred during the laying period (time between the laying of the first and second egg), 44 (62%) during the first spell, 14 (20%) during the second spell, 9 (13%) during the following spells, and 1 (1.4%) occurred at an unidentified spell. Eight of the 10 birds that deserted later than the second spell did so after the average length of the incubation period had elapsed (mean = 52.12 days, SD = 7.68, *n* = 8). Thus, desertions are more likely to occur early

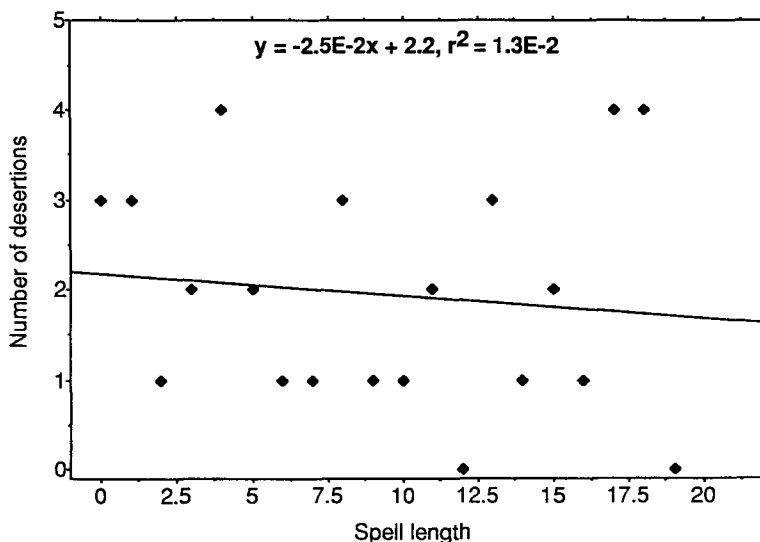


FIGURE 1. Distribution of nest desertions with respect to the length of time a bird incubated at each spell ( $r^2$ ,  $F = 0.5$ ,  $P = 0.49$ ). Desertions are pooled for male and female penguins, and for the first and second spells.

in incubation when the female is attending ( $\chi^2 = 6.26$ ,  $df = 1$ ,  $P = 0.01$ ).

Of the 68 deserted nests, 18 (26.5%) were early breeders, 24 (35.3%) were peak breeders, 22 (32.4%) were late breeders, and 4 (5.9%) could not be classified. Birds deserted independently of timing of egg laying ( $\chi^2 = 0.9$ ,  $df = 2$ , ns).

#### NEST-RELIEF HYPOTHESIS

The average length of the first two incubation spells was between 11 and 18 days and the females fast before egg laying until their relief in each year averaged 28 to 34 days (Table 2). Of the 39 females that deserted during egg laying or during the first spell, only 14 abandoned after incubating for longer than the average Spell 1 length; these females incubated from 1 to 6 days longer than average (mean = 3,  $SD = 2$ ,  $n = 14$ ). Three of the 12 males, deserting during the second incubation spell, left after incubating for longer than the average Spell 2 length; two of these males incubated for two days and one for 24 days longer than average. Of these males and females, 34 deserted after incubating for less than the average spell length and 17 deserted after incubating longer than the average ( $G$  test,  $G = 5.8$ ,  $df = 1$ ,  $P < 0.05$ ). Additionally, one female that took the second spell incubated for 20 days, a relatively long spell. Therefore, of all the deserting penguins, only 18 (25.4%) deserted after incubating for longer than the average spell length.

Six of these penguins incubated for one standard deviation longer than the average spell length.

The number of desertions was poorly correlated with spell length ( $r^2 = 0.02$ ; Fig. 1). Three birds deserted on the same day the eggs were laid. Thirteen (72%) of the 18 mates of penguins that deserted after longer than the average spell returned on average four days ( $SD = 2$ , range = 2–8 days) after the eggs were deserted. Of the four mates that were not seen again in the corresponding season, two were seen on the following year and two were not seen again in the following five seasons. The remaining mate was unbanded, and could not be identified again.

If desertion is mainly due to unusually long fasting periods, then desertion during Spell 1 should be closely related to the bird's fasting period. Time spent fasting on land, from arrival to desertion, was known for 35 of the 40 females that deserted during egg laying or during the first spell. Contrary to the prediction, only 11 (31.4%) of these 35 females had fasted longer than average, and except for one female, all were the same birds that incubated for longer than the average Spell 1. Only two of these females stayed at their nest for one standard deviation longer than the mean fasting time. Additionally, all five males that took the first incubation spell were assumed to have fasted for longer than average. Combining these birds with the 18 that incubated for longer than the average spell length,

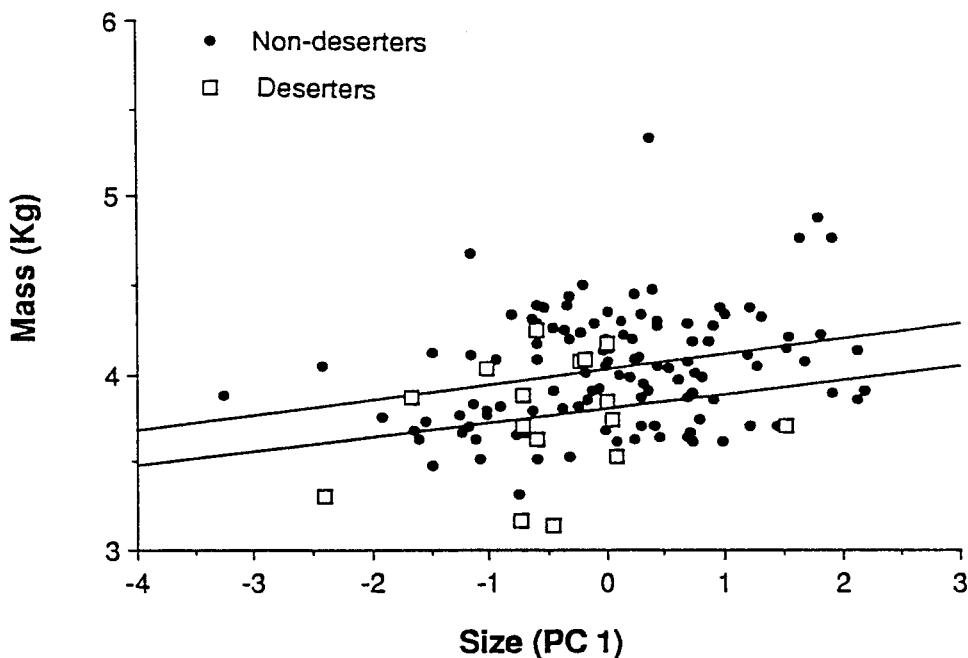


FIGURE 2. Differences in body condition of female Magellanic Penguins that deserted and did not desert during incubation. Body mass (kg) is plotted against a body size index (PC1). Non-deserters: mass (kg) =  $4.029 + 0.086 \times \text{PC1}$ . Deserters: mass (kg) =  $3.799 + 0.086 \times \text{PC1}$ .

the total number of birds that spent an unusually long time fasting at the nest was 24 (33.8%) out of 71 desertions.

#### BODY CONDITION HYPOTHESIS

The estimate of female body mass at the time of egg laying was dependent on when birds were weighed. Average daily mass loss from egg laying through the first spell varied significantly depending on how long before egg laying females arrived (ANOVA  $F = 6.34$ ;  $df = 2, 95$ ;  $P = 0.003$ ). Average mass loss per day was 53 g (SD = 14,  $n = 57$ ) for the period before the first egg was laid, 48 g per day (SD = 17,  $n = 23$ ) for the first week of incubation after the second egg was laid, and 40 g per day (SD = 6,  $n = 18$ ) for the second week of incubation.

A linear model showed a significant positive relationship between body size and mass at laying ( $r^2 = 0.4$ , ANOVA  $F_{3,127} = 6.6$ ,  $P < 0.001$ ,  $n = 131$ ). Regression slopes for deserters and non-deserters did not differ from parallel (Partial  $F$  test,  $F_{1,127} = 0$ , ns; Fig. 2). Birds that deserted were lighter for their body size at the time of egg laying than the penguins that did not desert (ANCOVA  $F_{1,128} = 7.1$ ,  $P < 0.01$ ; Fig. 2). At the

average body size for all birds, the difference in weight between deserters and non-deserters was 230 g.

#### WEATHER FACTORS AFFECTING DESERTION

Rainfall at Punta Tombo is irregular and scarce, with an average annual rainfall of approximately 200 mm. Storms can be severe and maximum rainfall was 30 mm in one day. Heavy rainfall can fill nests. Significant rain storms during the incubation period occurred in three of the seven years: 1984, 1985, and 1989. During these three years, from a total of 277 active nests at the time rains occurred, 27 (9.8%) were flooded and only 9 of these were deserted (5 in 1984, 1 in 1985, and 3 in 1989). Flooded nests were more likely to be deserted by the incubating bird than non-flooded nests ( $\chi^2 = 13.9$ ,  $df = 1$ ,  $P < 0.001$ ). Two other birds deserted when their burrow nests collapsed during a storm in 1985.

Nest desertions were not more likely to occur on the hottest days. Maximum temperatures for October and November were 29°, 27.5°, 29°, and 34°C for 1984, 1985, 1986, and 1989 respectively. Maximum temperatures on days when

desertions occurred were similar to maximum temperatures when no desertion occurred (Mann-Whitney  $U$ -test, 1984:  $U = -0.2$ ,  $n = 32,8$ , ns; 1985:  $U = -0.5$ ,  $n = 28,7$ , ns; 1986:  $U = -0.9$ ,  $n = 29,5$ , ns; 1989:  $U = -1.7$ ,  $n = 33,5$ , ns).

#### DISTURBANCE

Seven penguins fled at the approach of the researchers during the seven years of daily checks in the study area which included more than one hundred nests. None of these birds abandoned the nests for more than one day. Penguins that fled were more likely to be lighter for their body size at the time of egg laying than penguins that did not flee ( $\chi^2 = 4.8$ ,  $df = 1$ ,  $P = 0.03$ ).

#### DISCUSSION

Nest desertion is highly variable among species of penguins. Nest desertion rates during incubation were 21% in the Adelie Penguin *Pygoscelis adeliae* (Davis 1982), and 3% in the Yellow-eyed Penguin *Megadyptes antipodes* (Seddon 1989). Boersma (1976, 1978) found that during El Niño-Southern Oscillation events, Galapagos Penguin *Spheniscus mendiculus* deserted over 80% of the nests, during incubation and the early chick stage. Scolaro (1984) reported a nest desertion rate for the Magellanic Penguin of 32% ( $n = 19$ ). This is higher than the desertion rate in each of the seven years of our study and almost three times our average rate. The high rate Scolaro (1984) reported may have been influenced by his small sample size. Of the six nests scored as deserted, 4 (67%) occurred when the incubating bird was not relieved on time. His checking frequency which is unknown and reported as "closely monitored" may have caused him to score nests that failed from other causes as deserted which would lead to an inflated desertion rate.

The present study in contrast may have underestimated the desertion rate, as we only scored eggs as deserted if they were left unattended for two consecutive checks. In the seven years of the study only 14 nests had eggs and adults gone on the same check. These nests were scored as eggs preyed upon while attended, but, eggs in these nests could have disappeared soon after being deserted and, thus, may have been deserted and scavenged but not lost to predators. Even if all these cases are considered as desertion, the corrected average desertion rate is only 13%, suggesting our scoring was probably not a problem.

Nest desertion due to delayed nest relief has been described for several penguin species (Cooper 1980, Davis 1982, Lishman 1985, Groscolas 1990). Davis (1982) showed that delayed nest relief accounted for 89% of nest desertions in the Adelie penguin, resulting mainly from the depletion of the incubating mate's fat reserves. Desertions in Magellanic Penguins were affected by many different factors, and only 25% of the total desertions could be attributed to birds having longer than average incubation spells. If spells one standard deviation longer than average spell length are used as the criteria for unusually long spells, instead of the average spell, then only 8.5% of the desertions can be attributed to a delayed nest relief. Moreover, almost half of the nest desertions occurred before half the average spell length. Thus, less than 25% of birds appeared to desert because of a long incubation spell.

Penguins could take longer spells than average if the mate is delayed from its foraging trip. However, longer than average spells could also be the result of mate desertion or mortality. The mates of four of the eighteen birds that deserted after longer than average spells did not return to their nests that season. Two were not seen again over the next five breeding seasons and probably died. Two others were seen at the colony in the following season, suggesting they had deserted the breeding attempt.

If nest desertion is caused by the depletion of fat reserves, penguins should desert because of poor body condition; desertion should not be restricted to birds with unusually long incubation spells. Our results confirm this. Desertion was unrelated to length of spell, and females that deserted weighed less for their body size than birds that successfully completed incubation. This suggests that poor condition at the onset of breeding was the main reason for desertion. Williams and Croxall (1991) showed that Macaroni Penguins (*Eudyptes Chrysolophus*) can extend their fast if a mate is delayed in returning and that mate return time was a poor predictor of failed and successful nests. Their data suggest that delayed nest relief is not important in causing desertion in Macaroni Penguins.

Nest desertion may be caused by several other factors. Desertion following human disturbance is common for some seabird species (see review in Anderson and Keith 1980). The birds that neglected their eggs for one day several times before finally deserting and birds that returned

to resume incubation after less than four days (probably too short a period to replenish their fat reserves) suggest disturbance may have induced abandonment. A bird in poor body condition should be more inclined to leave the nest when threatened by human approach than if it were healthy. Penguins that abandoned the nest when approached were lighter for their body size than birds that did not flee, suggesting that body condition interacts with disturbance to cause desertion.

Weather factors, such as extreme weather conditions, can also be a cause of nest desertions (Yorio and Boersma, in press). Only a small percentage of desertion was caused either by rain flooding nests or because burrows collapse during the storms. Three of the penguins that deserted from flooded nests were in poor body condition or had incubated for longer than the average incubation spell, again pointing out that there are interactions among factors in determining nest desertion. Body condition appears to be very important in determining whether a penguin deserts and becomes more important when coupled with other factors. Penguins that breed in temperate, subtropical and tropical climates exhibit several adaptations to cope with breeding in hot environments (Frost et al. 1976). Heat stress is known to cause desertions in Galapagos (Boersma 1976) and Black footed penguins (La Cock 1988). Even though at Punta Tombo ambient maximum temperatures can be high, high temperatures did not increase desertion during incubation. Heat stress does not appear to be an important force affecting nest desertions in Magellanic Penguins nesting in bushes and burrows.

In summary, desertion in Magellanic Penguins is rare and is similar among early and late breeding pairs. Desertion, although uncommon, occurs when birds are in poor condition. Poor condition, and not long incubation stints, is the main reason why Magellanic Penguins desert. Other factors, such as flooding and human disturbance, can foster desertion but in general these factors are relatively unimportant and in most cases interact with poor body condition to influence a bird's decision to desert.

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#### LITERATURE CITED

- ANDERSON, D. J. 1989. Differential responses of boobies and other seabirds in the Galapagos to the 1986-87 El Niño-Southern Oscillation event. *Mar. Ecol. Prog. Ser.* 52:209-216.
- ANDERSON, D. W., AND J. O. KEITH. 1980. The human influence on seabird nesting success: conservation implications. *Biol. Conserv.* 18:65-80.
- BECK, J. R., AND D. W. BROWN. 1972. The biology of Wilson's Storm Petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Scient. Rep.* 69:1-54.
- BOERSMA, P. D. 1976. An ecological and behavioral study of the Galapagos Penguin. *Living Bird* 15: 43-93.
- BOERSMA, P. D. 1978. Breeding patterns of Galapagos Penguins as an indicator of oceanographic conditions. *Science* 200:1481-1483.
- BOERSMA, P. D., D. L. STOKES, AND P. M. YORIO. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina, p. 15-43. *In* L. S. Davis and J. T. Darby [eds.], *Penguin biology*. Academic Press, San Diego, CA.
- BOSWALL, J., AND D. MACIVER. 1975. The Magellanic Penguin *Spheniscus magellanicus*, p. 271-305. *In* B. Stonehouse [ed.], *The biology of penguins*. Macmillan, London.
- BUCKLEY, F. G., AND P. A. BUCKLEY. 1972. The breeding ecology of Royal Terns *Sterna (Thalasseus) maxima maxima*. *Ibis* 114:344-359.
- COOPER, J. 1980. Breeding biology of the Jackass Penguin with special reference to its conservation. *Proc. IV Pan-Afr. Orn. Congr.* 227-231.
- DAVIS, L. S. 1982. Timing of nest relief and its effect on breeding success in Adelie Penguins (*Pygoscelis adeliae*). *Condor* 84:178-183.
- DAVIS, L. S. 1988. Coordination of incubation routines and mate choice in Adelie Penguins (*Pygoscelis adeliae*). *Auk* 105:428-432.
- DUFFY, D. C. 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64: 110-119.
- EMLEN, J. T., D. E. MILLER, R. M. EVANS, AND D. H. THOMPSON. 1966. Predator-induced parental neglect in a Ring-billed Gull colony. *Auk* 83:677-679.
- FISHER, H. I. 1971. The Laysan Albatross: its incubation, hatching, and associated behaviors. *Living Bird* 10:19-78.
- FROST, P. G. H., W. R. SIEGFRIED, AND A. E. BURGER. 1976. Behavioral adaptations of the Jackass Penguin *Spheniscus demersus* to a hot, arid environment. *J. Zool. (London)* 179:165-187.
- GROSCOLAS, R. 1990. Metabolic adaptations to fasting in Emperor and King penguins, p. 269-296.

- In L. S. Davis and J. T. Darby [eds.], Penguin biology. Academic Press, San Diego, CA.
- JOUVENTIN, P. 1975. Mortality parameters in emperor penguins *Aptenodytes forsteri*, p. 435-446. In B. Stonehouse [ed.], The biology of penguins. Macmillan, London.
- KING, K. A., D. R. BLANKINSHIP, AND R. T. PAUL. 1977a. Ticks as a factor in the 1975 nesting failure of Texas Brown Pelicans. *Wilson Bull.* 89:157-158.
- KING, K. A., J. O. KEITHE, AND G. A. MITCHELL. 1977b. Ticks as a factor in nest desertion of California Brown Pelicans. *Condor* 79:507-509.
- LA COCK, G. D. 1988. Effect of substrate and ambient temperature on burrowing African Penguins. *Wilson Bull.* 100:131-132.
- LISHMAN, G. S. 1985. The comparative breeding biology of Adelie and Chinstrap penguins *Pygoscelis adeliae* and *P. antarctica* at Signy Island, South Orkney Islands. *Ibis* 127:84-99.
- NELSON, J. B. 1978. The sulidae. Oxford Univ. Press, Oxford, U.K.
- SCOLARO, J. A. 1984. Timing of nests relief during incubation and guard stage period of chicks in Magellanic Penguin (*Spheniscus magellanicus*) (Aves: *Spheniscidae*). *Hist. Nat.* 4:281-284.
- SEDDON, P. 1989. Patterns of nest relief during incubation, and incubation period variability in the Yellow-eyed Penguin (*Megadyptes antipodes*). *N. Z. J. Zool.* 16:393-400.
- SHEALER, D. A., AND S. W. KRESS. 1991. Nocturnal abandonment response to Black-crowned Night-Heron disturbance in a Common Tern colony. *Colon. Waterbirds* 14:51-56.
- WILLIAMS, T. D., AND J. P. CROXALL. 1991. Annual variation in breeding biology of Macaroni Penguins, *Eudyptes chrysolophus* at Bird Island, South Georgia. *J. Zool. Longon.* 223:189-202.
- YORIO, P. M., AND P. D. BOERSMA. In press. Consequences of nest desertion and inattendance for Magellanic Penguin hatching success. *Auk*.
- YORIO, P. M., AND P. D. BOERSMA. 1992. The effects of human disturbance on Magellanic Penguin *Spheniscus magellanicus*. *Bird Conservation International* 2:161-173.