

TIMING OF NEST RELIEF AND ITS EFFECT ON BREEDING SUCCESS IN ADELIE PENGUINS (*PYGOSCELIS ADELIAE*)

LLOYD S. DAVIS

ABSTRACT.—I determined the fates of 259 eggs laid by 130 pairs of banded Adelie Penguins (*Pygoscelis adeliae*) at Cape Bird, Antarctica (77°13'10"S, 166°28'30"E). Failure of penguins to return from feeding at sea in time to relieve their mates at the nest resulted in the desertion of 48 eggs (47.5% of all egg losses) and the starvation of 29 chicks (35.4% of all chick losses). Eggs were more likely to be deserted if they belonged to parents that had bred either very early or very late. Most eggs were deserted when females did not return in time to relieve their mates from the First Incubation Spell, so that the risk of desertion became appreciable only after the eggs were 16 days old. Starvation was especially likely when chicks were 6-8 days old, largely because males did not return to relieve the females, particularly from the Second Incubation Spell. Pairs that successfully completed nest relief regulated the total duration of the First and Second Incubation Spells, keeping it slightly less than the duration of the incubation period.

Eggs and chicks of Adelie Penguins (*Pygoscelis adeliae*) are lost in considerable numbers, yet the causes and dimensions of mortality have had little direct study. Most information on the subject has hitherto been gained incidentally during studies of other aspects of the birds' biology. Many workers have provided gross estimates of breeding success, but only Taylor (1962) and Spurr (1975) attempted to quantify factors responsible for egg and chick losses. However, in even the most detailed of these studies (Spurr 1975), the cause of mortality and the age at which it occurred were monitored only at 10-day intervals for eggs and five-day intervals for chicks. As a result, fully 59% of egg losses and 20% of chick losses were to unknown causes. Spurr did note that desertion and starvation were major causes of egg and chick mortality, respectively, but he could not ascertain the reason for most of the desertions, and thought starvation resulted solely from the death of one parent. Although Yeates (1968) proposed that long incubation spells increase the incidence of desertion, researchers have neither suggested that Adelie Penguins are able to regulate the length of their incubation spells, nor presented any direct evidence that the timing of nest relief is responsible for desertion and starvation.

I monitored the survival of a large sample of eggs and chicks by keeping them under regular and frequent surveillance and in this way was able to determine the causes of mortality more accurately than has been done previously. I followed the nest relief cycles of pairs of penguins in which the individuals were readily distinguishable because at least one of the pair was banded.

METHODS

I monitored fates of 259 eggs belonging to 130 pairs of Adelie Penguins in H-block of the Northern Rookery (Knox and Ensor 1978), Cape Bird, Ross Island, Antarctica (77°13'10"S, 166°28'30"E) during a study carried out there between 23 October 1977 and 24 January 1978. At least one member of each pair was marked with aluminum alloy flipper bands, of the type used by the U.S.A.R.P. Bird Banding Program (Sladen and LeResche 1970), and its back was painted with a coded combination of a letter and numerals, before breeding began. Sex was determined either from copulatory position or a combination of behavioral criteria (Sladen 1958:23-24).

H-block contained 452 nests in six colonies. Locations of all nests, including the 130 belonging to the banded pairs, were mapped with reference to rock markers and surrounding nests. I inspected the nests in sequence each morning, usually from 09:00 to 12:00. I could often see the contents of a nest if the attending bird altered its position on it. In most cases, however, I used a long bamboo pole to slightly lift the rear ends of nesting penguins and expose the nest's contents. This minimized disturbance to the birds since, in contrast to other studies (Penney 1968, Tenaza 1971), I did not enter the colonies and the penguins remained on their nests.

I recorded dates of laying and hatching for all eggs; dates and reasons for the loss of any egg or chick; and, in the case of the banded pairs, the identities of the attending bird and the dates of nest relief. "Very early" and "very late" breeders were defined as pairs whose first

egg was laid earlier or later, respectively, than one standard deviation from the mean date for first eggs. I restrict this paper to the fates of those eggs and chicks of pairs in which at least one member was banded, due to the unequivocal nature of the evidence, although I found no significant difference in the proportion of chicks that fledged (i.e., were alive on 24 January) from the eggs of banded and unbanded pairs ($\chi^2 = 3.12$, $P > 0.05$).

I define the "First Incubation Spell" (FIS) as the period from the laying of the last egg in the clutch until the sitting bird is relieved by its mate. The "Second Incubation Spell" (SIS) begins then and continues until the first bird returns and takes over the nest again. To establish the normal mean duration of the FIS and SIS, I considered only those pairs that successfully completed both spells, and in which the male incubated first.

To compute the risk of desertion and starvation for eggs and chicks, respectively, I used the SPSS computer program "survival" (Hull and Nie 1979), which evaluates the elapsed time between a starting event (laying or hatching) and a terminal event (desertion or starvation). The survival of the 259 eggs and 158 chicks of the banded pairs was examined at age intervals of two days. For each interval, the number of eggs or chicks exposed to risk was calculated as the number entering the interval minus one-half the number dying during that interval of causes other than desertion or starvation (or those eggs that hatched, or chicks that fledged [survived to 24 January]). (Eggs incubated for longer than 38 days after the completion of the clutch [$n = 10$] were assumed to have been addled or infertile, and were treated arbitrarily in the analysis as having been lost within the two-day interval immediately following laying.) The hazard rate was then computed as the proportion of those exposed to risk that died of desertions or starvations in a given interval, divided by the average number of survivors at the mid-point of that interval. This hazard function gives the probability that an individual egg or chick, which has survived to the beginning of a two-day interval, will die of desertion or starvation within that interval.

To determine the disturbance that my frequent observations had on H-block, I used 39 colonies in A-, B-, C-, and G-blocks of the rookery as a control group that I visited only twice during the study. The first visit was between 28–30 November, at which time the number of nests with an adult in attendance (the number of occupied nests) in each colony was counted. This figure closely approximated the number of incubating pairs present, since

most non-breeders were absent at that time (Penney 1968). The control colonies were visited again between 20–21 January, at which time I recorded the number of chicks present. I followed identical procedures for the colonies in H-block. Breeding success was then expressed as the number of chicks alive on 20–21 January per occupied nest on 28–30 November, which is an approximate estimate of the number of chicks fledged per nest. Although the average breeding success for colonies in H-block (0.73 chicks/occupied nest) was slightly less than that in the control colonies (0.88 chicks/occupied nest), this difference is not significant ($P > 0.05$, Mann-Whitney U -test [one-tailed]), and may be related to the high density of South Polar Skuas (*Catharacta maccormicki*) then present in H-block compared to the rest of the rookery (Davis 1980).

RESULTS

Adelie Penguins began to arrive at H-block on 24 October. Males usually returned to the rookery before their mates (in 16 [67%] of 24 cases where one member of a pair was known to have been in the colony before the other) and selected nest sites. When the females arrived, the birds went through a period of courtship which averaged 11 days (range 8–16 days, $n = 31$) until the eggs were laid (6 Nov. to 1 Dec., $\bar{x} = 12.6$ Nov. for first eggs, $SD = \pm 3.8$ days, $n = 452$). Females then went to sea, leaving the males to incubate (FIS). After an average of 16.6 days (range 9–25 days, $n = 84$), the females returned and relieved their mates. Females were subsequently alone at their nests (SIS) for an average of 12.3 days (range 7–20 days, $n = 84$). Once males returned from feeding, the mates alternated attendance at their nests much more frequently (Fig. 1). Chicks hatched soon after the SIS, following an incubation period of about 34 days ($\bar{x} = 33.7$ days for second eggs in the clutch, $SD = \pm 1.1$ day, range 32–38 days, $n = 192$). Frequent changes of the brooding parent continued until the end of the "guard stage" (Richdale 1957) when chicks averaged 22 days of age (range 16–34 days, $n = 23$). Thereafter, both parents were usually away from the nest simultaneously (the "creche stage" [Sladen 1958]).

In 8 of the 130 banded pairs (6.2%), males went to sea first, but were away so briefly that the average FIS was only 4.2 days (range 2–7 days, $n = 6$; the clutches of the other two males were lost before they returned). All of these males had been at the colony for a longer period than that normally required for courtship ($\bar{x} = 19$ days, range 17–22 days, $n = 8$). Under these circumstances, males might require a brief period to forage at sea to replenish fat

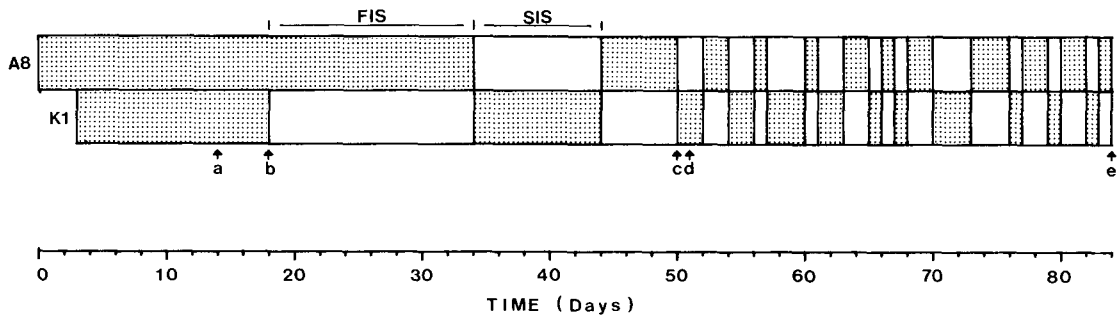


FIGURE 1. Nest relief pattern of a banded pair of Adelle Penguins, male A8 and female K1, showing the First and Second Incubation Spells (FIS and SIS) followed by a more rapidly cycling phase of nest relief. The stippled area represents the time at the nest. Also indicated are the days on which the eggs were laid (a and b), the chicks hatched (c and d), and the "guard stage" ended (e). Time 0 was 26 October 1977.

reserves depleted by the long "courtship period" before they begin to incubate.

Of 259 eggs laid by the banded pairs (4 one-egg clutches, 123 two-egg clutches, and 3 three-egg clutches in which the third egg was laid after the first was lost within 48 h), 48 (from 27 nests) were deserted because a mate did not return in time to relieve its partner on the nest. Thus, these desertions accounted for 18.5% of all eggs laid, and 47.5% of all egg losses.

Most of the desertions (85%) occurred after the mean FIS and before the end of the mean SIS (Fig. 2). My finding that 22 (81%) were desertions by males that had been on the nest for *longer* (up to 29 days) than the average FIS, without being relieved by their mates, indicates that the timing of nest relief is critical in precipitating desertions. Of those late females, eight (36%) were seen at the rookery after their mates deserted the nest. On the other hand, the two desertions that occurred after the mean SIS (day 35 and 36) were both by females whose males were late returning. The two seemingly anomalous desertions that occurred *before* the end of the mean FIS (day 13) involved unusual incubation routines in which the female took the FIS.

Since desertions usually resulted only when females were late in relieving their mates from the FIS, the hazard to the eggs was virtually nil until they were 16 days old (Fig. 3). Thereafter, the hazard increased rapidly, and was greatest when eggs were 22–24 days old. The risk of desertion then subsided briefly, reaching a low level at 30 days, followed by another peak at 36 days. Males who did not return in time to relieve females from the SIS (Fig. 2) were responsible for this second peak. Although the *number* of desertions at that time was small, most of the eggs had already hatched, so that for those few remaining the hazard of desertion was high.

Pairs that nested very early (on or before 8 Nov.) or very late (17 Nov. or later) were much more likely to desert ($\chi^2 = 6.83$, $P < 0.01$) than those that nested within one standard deviation (9–16 Nov.) of the mean laying date.

Twenty-nine (18.4%) chicks from 16 nests, of the 158 that hatched, died of starvation, which accounted for 35.4% of all chick losses. Starvations occurred when a bird failed to return to the nest in time, thereby leaving its mate to guard the chicks and consequently unable to feed them. The risk of starvation was

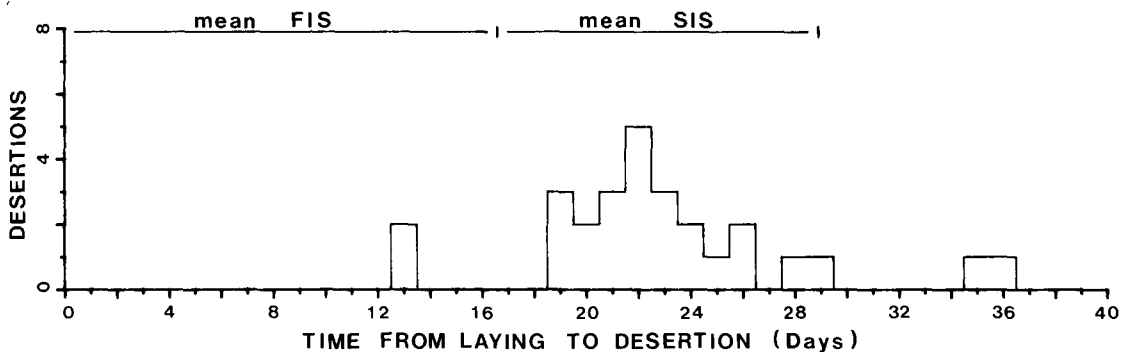


FIGURE 2. The frequency of desertion with respect to the time the clutches had been incubated after the completion of laying ($n = 27$). Mean duration of the First (FIS) and Second (SIS) Incubation Spells was 16.6 and 12.3 days, respectively.

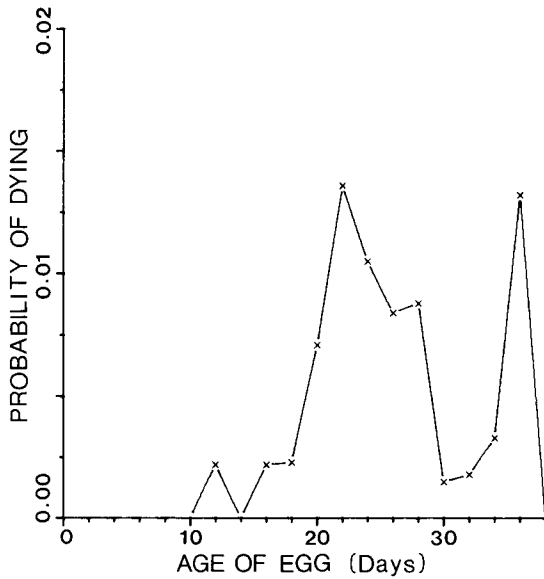


FIGURE 3. Hazard function, calculated from a sample of 259 eggs belonging to 130 banded pairs of Adelie Penguins, showing the probability that an individual egg that has survived to the beginning of each two-day interval will die from desertion within that interval.

especially high when chicks were 6–8 days old (Fig. 4), remained relatively high until they were 16 days old, and declined thereafter to the end of the “guard stage.” At that point, a parent was no longer bound to stay and guard the chick(s), and could feed them alone in the absence of its mate. Presumably, starvations could occur during the “creche stage” only in the uncommon event that both parents fail to return to the colony. In 12 (75%) of the 16 nests in which chicks starved, males did not return to relieve the females, half of which had not been relieved from the SIS.

There was considerable variation in the duration of both the FIS ($\bar{x} = 16.6$ days, variance = 13.8 days, $n = 84$) and SIS ($\bar{x} = 12.3$ days, variance = 8.4 days, $n = 84$) in pairs that completed both of them. The *sum* of the two incubation spells for each pair, however, was much less variable ($\bar{x} = 28.9$ days, variance = 6.9 days, $n = 84$). In other words, if a female spent a longer than average time at sea, her mate spent less than the average time, and vice versa ($r = -0.71$, $P < 0.001$, $y = 21.52 - 0.56x$, $n = 84$).

DISCUSSION

Taylor (1962) considered desertions to be a major cause of egg losses among Adelie Penguins, but thought that they resulted either from the inexperience of the parents or flooding of nests by thaw water. Spurr (1975) found that desertions (87% from unknown causes) accounted for 28% of egg losses, and perhaps

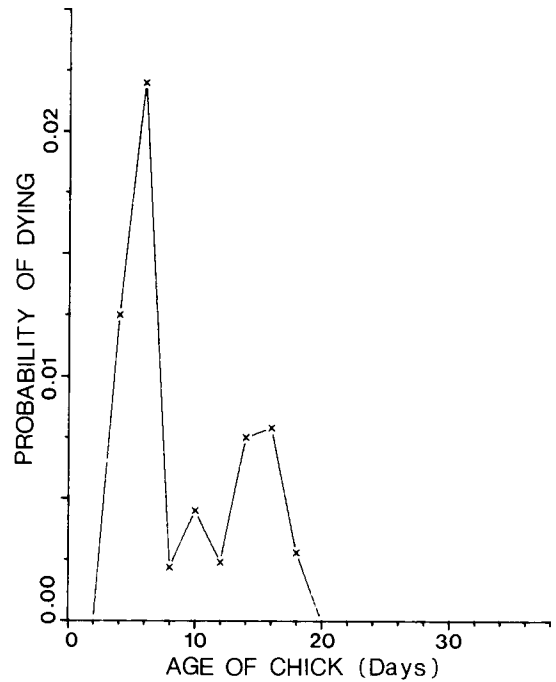


FIGURE 4. Hazard function, calculated from a sample of 158 chicks, showing the probability that an individual chick that has survived to the beginning of each two-day interval will die from starvation within that interval.

more, since an additional 35% of all eggs lost disappeared for unknown reasons. However, simply attributing losses to desertion provides little information about factors that influence egg survival, unless the causes of the desertions are known, since eggs may be lost before the parent deserts (e.g., to skuas), and the parent may desert for several reasons (e.g., hunger, cold).

From my results, the common characteristic of deserting parents was the fact that they had been incubating for an abnormally long time, apparently because their mates had not returned to relieve them. Desertion may therefore be a response to the depletion of their fat reserves. Fasting adult Adelie Penguins lose about 56 g/day, and after 27 days (the approximate time normally taken for courtship and the FIS) the fat reserves of males have decreased by more than half (Johnson and West 1973). My results contradict Young's (1963:308) assertion that many eggs are subject to desertion during the *first week* of incubation, since the hazard of desertion became appreciable only after eggs were 16 days old (i.e., after the mean length of the FIS).

On the basis of only a few observations, Sapin-Jaloustre (1960) believed that eggs were deserted when females were absent and males were fasting (taking the FIS). Yeates (1968, 1975) suggested a connection between the tim-

ing of nest relief and the incidence of desertion, arguing that longer incubation spells increased the latter. He thought, however, that the duration of the incubation spell was mediated by the climate and he did not propose that penguins themselves regulate the length of their trips away from the nest (Yeates 1971).

Birds that have the best sense of time might reasonably be expected to breed when it is most opportune, since the period of breeding for Adelie Penguins is determined by a common environmental trigger (Spellerberg 1971). Pairs with the best timing should be those that breed near the norm (the implied optimum). This would explain why desertions were most prevalent in pairs that bred very early or very late. Young birds tend to breed very late (Davis 1980), because the members of young breeding pairs are less synchronous in their arrival at the rookery than are older pairs (LeResche and Sladen 1970), i.e., have poorer timing abilities. (Newly formed pairs of Black-legged Kittiwakes [*Rissa tridactyla*] also cannot co-ordinate their incubation pattern as well as long established pairs [Coulson 1966].)

My results are consistent with those of Spurr (1975), who found that 30% of chick deaths were due to starvation. However, he assumed that such deaths were caused exclusively by the loss of one parent, rather than by poor timing of nest relief by the parent birds. Newly hatched chicks can survive unfed for 5.5 to 8 days (Reid and Bailey 1966). In my study, the hazard of starvation was especially high when the chicks were six to eight days old. That is, most starvations occurred when chicks were not fed upon hatching, because one parent (usually the male) failed to return from feeding at sea on time (or at all), in which case its fasting mate (often the female taking the SIS) was left to guard the nest and was consequently unable to feed them. Spurr (1975) also found that chicks starved only during the "guard stage." Once both parents are emancipated from guard duties, each can feed the chick(s) in the absence of its mate, and the timing of nest relief ceases to be a mortality factor.

Evidently, many of the tardy parents were alive. Thirty-six percent of the females who were late were seen at the rookery subsequent to the desertions of their mates. Furthermore, the average mortality during the breeding season at Cape Bird is only 3.8% for males and 4.6% for females (Spurr 1975), and consequently too low to account for the 33% (43/130) of all nests afflicted by desertions and starvations.

The timing of nest relief is apparently critical, but for reasons that differ, at least initially, between the sexes. The female must return

from her first spell at sea before the male's fat reserves are depleted, which is especially critical because he has already fasted for approximately two weeks before he begins the FIS. On the other hand, the female has recently renewed her fat deposits when she begins the SIS, and it is unlikely that she will desert until well after the eggs hatch. Hence, it is necessary that the male return, not before the female's fat reserves are consumed, but before the chicks' yolk sacs are depleted, so that they will not starve.

It is essential, therefore, that the parents reach the stage of the cycle when nest reliefs are frequent by the time the eggs hatch. Herein lies the adaptive advantage of having the FIS and SIS sum, with as little variation as possible, to slightly less than the incubation period of the eggs. To achieve this, the male, at least, must have a sense of timing, such as an endogenous biological clock, which enables him to measure the duration of the incubation period.

Emlen and Penney (1964) showed that Adelie Penguins do possess a biological clock. Furthermore, diurnal rhythms have been demonstrated for movements to (Spurr 1978) and from (Muller-Schwarze 1968, Paulin and Sagar 1977, Davis 1980) the rookery, and in the number of upright movements made by incubating birds (Derksen 1977).

My data also suggest that individual penguins have a sense of time, and why: for the Adelie Penguin, breeding success is apparently determined to a large extent by the timing of nest relief.

ACKNOWLEDGMENTS

I am grateful to M. C. Crawley and J. Warham for advice, encouragement, and constructive criticism of the manuscript. M. Wenden helped band the penguins, G. Wilson directed the census of occupied nests, and together with P. Ensor and E. Waghorn provided warm companionship at Cape Bird.

This study was carried out while I was a member of the Antarctic Research Unit of the University of Canterbury, Christchurch, New Zealand. Field support was provided by the Antarctic Division of the Department of Scientific and Industrial Research, and logistic support by the U.S. Navy VXE-6 squadron.

LITERATURE CITED

- COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *J. Anim. Ecol.* 35:235-238.
- DAVIS, L. S. 1980. Egg and chick survival of the Adelie Penguin (*Pygoscelis adeliae*) at Cape Bird, Antarctica. M.Sc. thesis, Univ. of Canterbury, Christchurch, New Zealand.
- DERKSEN, D. V. 1977. A quantitative analysis of the incubation behavior of the Adelie Penguin. *Auk* 94:552-566.
- EMLÉN, J. T., AND R. L. PENNEY. 1964. Distance navigation in the Adelie Penguin. *Ibis* 106:417-431.

- HULL, C. H., AND N. H. NIE. 1979. SPSS update. McGraw-Hill, New York.
- JOHNSON, S. R., AND G. C. WEST. 1973. Fat content, fatty acid composition and estimates of metabolism of Adelie Penguins (*Pygoscelis adeliae*) during the early breeding season fast. *Comp. Biochem. Physiol. B* 45:709-719.
- KNOX, G. A., AND P. H. ENSOR. 1978. University of Canterbury Antarctic Research Unit Expedition 16. Department of Zoology, University of Canterbury, Christchurch, New Zealand.
- LERESCHE, R. E., AND W. J. L. SLADEN. 1970. Establishment of pair and breeding site bonds by young known-age Adelie Penguins (*Pygoscelis adeliae*). *Anim. Behav.* 18:517-526.
- MULLER-SCHWARZE, D. 1968. Circadian rhythms of activity in the Adelie Penguin (*Pygoscelis adeliae*) during the austral summer, p. 133-149. In O. L. Austin [ed.], *Antarctic bird studies*. Antarctic Research Series. Vol. 12. American Geophysical Union, Washington, DC.
- PAULIN, C. D., AND P. M. SAGAR. 1977. A diurnal rhythm of activity by the Adelie Penguin. *Notornis* 24:158-160.
- PENNEY, R. L. 1968. Territorial and social behavior in the Adelie Penguin, p. 83-131. In O. L. Austin [ed.], *Antarctic bird studies*. Antarctic Research Series. Vol. 12. American Geophysical Union, Washington, DC.
- REID, B., AND C. BAILEY. 1966. The value of the yolk reserve in Adelie Penguin chicks. *Rec. Dom. Mus. (Wellington)* 5:185-193.
- RICHDALE, L. E. 1957. A population study of penguins. Clarendon Press, Oxford.
- SAPIN-JALOUSTRE, J. 1960. *Ecologie du Manchot Adelie*. Hermann, Paris.
- SLADEN, W. J. L. 1958. The pygoscelid penguins I: Methods of study, II: The Adelie Penguin. *Falkland Isl. Depend. Surv. Sci. Rep.* 17:1-97.
- SLADEN, W. J. L., AND R. E. LERESCHE. 1970. New and developing techniques in Antarctic ornithology, p. 585-596. In M. Holdgate [ed.], *Antarctic ecology*. Academic Press, London.
- SPELLERBERG, I. F. 1971. Arrival and departure of birds at McMurdo Sound, Antarctica. *Emu* 71:167-171.
- SPURR, E. B. 1975. Breeding of the Adelie Penguin *Pygoscelis adeliae* at Cape Bird. *Ibis* 117:324-338.
- SPURR, E. B. 1978. Diurnal activity of Adelie Penguins *Pygoscelis adeliae* at Cape Bird. *Ibis* 120:147-152.
- TAYLOR, R. H. 1962. The Adelie Penguin *Pygoscelis adeliae* at Cape Royds. *Ibis* 104:176-204.
- TENAZA, R. 1971. Behavior and nesting success relative to nest location in Adelie Penguins (*Pygoscelis adeliae*). *Condor* 73:81-92.
- YEATES, G. W. 1968. Studies on the Adelie Penguin at Cape Royds 1964-65 and 1965-66. *N.Z. J. Mar. Freshwater Res.* 2:472-496.
- YEATES, G. W. 1971. Diurnal activity in the Adelie Penguin (*Pygoscelis adeliae*) at Cape Royds, Antarctica. *J. Nat. Hist.* 5:103-112.
- YEATES, G. W. 1975. Microclimate, climate and breeding success in Antarctic penguins, p. 397-409. In B. Stonehouse [ed.], *The biology of penguins*. Macmillan, London.
- YOUNG, E. C. 1963. Feeding habits of the South Polar Skua *Catharacta maccormicki*. *Ibis* 105:301-318.

Department of Zoology, University of Canterbury, Christchurch, New Zealand. Present address: Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. Received 17 June 1981. Final acceptance 11 January 1982.

Condor 84:183

© The Cooper Ornithological Society 1982

RECENT PUBLICATIONS

The Relationships of the Pedionomidae (Aves: Charadriiformes).—Storrs L. Olson and David W. Steadman. 1981. Smithsonian Contributions to Zoology No. 337, Smithsonian Institution Press, Washington, DC. 25 p. Paper cover. The Australian Plains-wanderer (*Pedionomus torquatus*) has been placed in a monotypic family long thought to be related to the button-quails, Family Turnicidae, now included in the Order Gruiformes. Stimulated by a 1969 study by W. J. Bock and A. McEvey which showed that its skeleton differs greatly from that of *Turnix*, Olson and Steadman undertook further comparisons of the bird. In this report on its osteological characters, they show it to be a charadriiform, most similar to the South American seedsnipes, Family Thinocoridae. *Pedionomus* tends to bridge the gap between that group and the more typical Charadriiformes. Photographs, references.

The Cuckoo.—Ian Wyllie. 1981. B. T. Batsford, Ltd., London. 176 p. £8.95. Of the approximately 80 species of brood parasitic birds known worldwide, the European Cuckoo (*Cuculus canorus*) shows some of the most advanced adaptations for the habit. Also, it has surely received the most attention. The making of a wildlife film about the bird led the author to a six-year field study of cuckoos parasitizing Reed Warblers (*Acrocephalus scirpaceus*), using marked individuals in Cambridgeshire, England. Drawing on his findings as well as the copious literature, he presents here a complete picture of the ecology and general biology of the species. Information about the cuckoo is supplemented with that on other cuckoos and other parasitic birds. Wyllie makes an effort to winnow facts from the many theories concerning the cuckoo's habits, and to confirm or refute speculations on the basis of careful observations. He illustrates his points with many remarkable photographs of birds at nests, in monochrome and in color. Students of cowbirds and other brood parasitic species will find a great deal of interest in this book. Scientific, yet understandable, it exemplifies an approach to natural history writing that is cultivated in Britain more than in the U.S. References, index.