COORDINATION OF INCUBATION ROUTINES AND MATE CHOICE IN ADÉLIE PENGUINS (PYGOSCELIS ADELIAE)

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ABSTRACT.—I studied the mating patterns and foraging-trip durations for a colony of Adélie Penguins (*Pygoscelis adeliae*) over two consecutive breeding seasons. Foraging-trip duration was not predicted by the time spent fasting before leaving the nest, but was consistent with the time remaining until hatching of the chicks. Consequently, foraging trips of pairs that successfully coordinated their incubation routine were complementary. The complementarity was due at least in part to the assortative effects of mate choice. Pairs that successfully coordinated the first three foraging trips remained together the next season; pairs that did not, separated. I argue that Adélie Penguins should retain their mates if partners are synchronous in their arrival at the rookery the next year and that, therefore, pairs unable to coordinate incubation must also be unlikely to coordinate their arrival at the rookery the next season. *Received 6 March 1987, accepted 25 January 1988.*

Most colonial seabirds exhibit a high degree of mate retention from one breeding season to the next (Rowley 1983, Cuthbert 1985). Breeding success is often higher for birds that retain their mates than for newly formed pairs (Coulson 1966, Mills 1973, Davis 1976, Brooke 1978, Ollason and Dunnett 1978, Boersma et al. 1980, Coulson and Thomas 1983). In Black-legged Kittiwakes (*Rissa tridactyla*) this is due partly to better coordination of nest relief between members of established pairs (Coulson 1966).

Failure of Adélie Penguins (*Pygoscelis adeliae*) to coordinate their nest-relief pattern results in desertion of eggs or starvation of chicks (Davis and McCaffrey 1986) in up to one-third of all nests (Davis 1982a). Adélie Penguins show low rates of mate retention, however (Ainley et al. 1983), relative to other colonial seabirds (Rowley 1983).

Incubation lasts about 34 days (Sladen 1958, Davis 1982b, Ainley et al. 1983) and typically involves three nest reliefs. After laying the female feeds at sea (the first foraging trip, FFT) and returns to relieve the male after about 2 weeks. The male then goes to sea (the second foraging trip, SFT) for approximately 2 weeks (Davis 1982a). Usually the female completes another, much shorter trip (the third foraging trip, TFT) before chicks hatch (Penney 1968). To successfully coordinate this pattern of nest relief, the duration of foraging trips for a pair must be complementary (Davis 1982a).

I monitored the degree of coordination of nest relief in a colony of Adélie Penguins under continuous observation for one season. I con-tinued to observe their mating and nest-relief patterns the next season to test whether coordinated nest-relief patterns result from mate choice for complementary partners.

I hypothesized that partners should reunite if they successfully coordinate nest relief, because this should produce further success. Others may profit most by separating, especially if individual foraging patterns are reasonably fixed; to be successful penguins would need to keep changing mates until paired with complementary partners. I predicted that pairs that successfully coordinate nest relief will stay together the next season, whereas others will change partners. A supporting, but not a mandatory prediction, was that the duration of foraging trips of individual penguins will be consistent between seasons.

METHODS

The study was undertaken in the Northern Rookery at Cape Bird, Ross Island, Antarctica (77°13'10"S, 166°28'30"E) during the 1984–1985 (31 October to 22 January) and 1985–1986 (15 November to 17 December) breeding seasons.

In 1984–1985 I banded all birds in the study colony before breeding began with individually numbered aluminium alloy flipper bands of the type used by the U.S.A.R.P. Bird Banding Program (Sladen and LeResche 1970). Coded alphanumeric combinations were painted on their backs to aid individual identification at a distance. Thereafter the colony was observed continuously by 5 persons in around-the-clock shifts from the beginning of the first FFT (6 November 1984) until the completion of the last TFT (24

December 1984). Severe storms on 9 and 13 November, which destroyed the observation tent, caused the only disruptions to an otherwise continuous sequence of observations. Sporadic observations were made of the colony during the few hours of interruption.

All arrivals and departures of penguins at the colony were recorded using all-occurrences sampling (Altmann 1974). The duration of each foraging trip (±1 min) was ascertained for members of each pair. Birds were sexed on the basis of copulatory position in combination with other behavioral criteria (Sladen 1958, Davis 1982a).

To assess any effects of constant surveillance on breeding success or foraging-trip durations, I established two controls. Nine colonies similar in size to the study colony were visited only twice: once to count the number of occupied nests and once to count chicks. Hatching success was expressed as the number of chicks (24 December) per occupied nest (26 November), and similar values were calculated for the study colony. Second, to determine whether foraging-trip durations of birds in the study colony matched those of birds in the rookery at large, patterns of nest attendance for 12 banded individuals in other colonies were noted by inspecting their nests only once per day.

In 1985–1986 I visited the study colony daily at 2300. I recorded the identities of banded birds, their partners, nest site, and pattern of nest attendance. Frequent searches of adjacent colonies for banded birds and a thorough colony-by-colony search of the entire rookery were conducted.

I used linear regression, Chi-square test with Yates' continuity correction factor, or Student's *t*-test for statistical comparisons. Two-tailed tests were employed unless *a priori* predictions justified the use of a one-tailed test. The nonparametric Mann-Whitney *U*-test was used where data were not normally distributed. To control for any variable effect of seasonal ice conditions on foraging times (Ainley and LeResche 1973), between-season comparisons used relative foraging durations (i.e. the rank order of foraging times for individuals of the same sex).

RESULTS

Coordination of incubation routines.—In the 1984–1985 breeding season, 38 pairs produced at least 1 egg in the study colony. The mean date for clutch initiation was 8 November (SD = 2.3 days, *n* = 38) and included 9 one-egg and 29 two-egg clutches.

Of the 38 pairs, 23 followed a normal incubation routine and successfully completed the FFT, SFT, and TFT (Table 1). The mean time elapsed from the beginning of the FFT to the end of the TFT for each pair was 34.9 days (Table

TABLE 1. Durations (in days) of first (FFT), second (SFT), and third (TFT) foraging trips for pairs of Adélie Penguins (*n* = 23) that successfully coordinated their incubation routine. Sum includes times for changeovers between foraging trips.

	FFT	SFT	TFT	Sum
Mean	19.02	12.60	3.14	34.90
SD	3.45	2.68	1.72	2.77

1). The duration of the SFT was significantly but negatively related to the duration of the FFT ($r = -0.55$, $P < 0.01$, $n = 23$) (Fig. 1). The mean incubation period from the completion of laying until hatching of the first chick was 33.8 days (SD = 1.6, $n = 20$; the eggs of 3 pairs were addled or infertile). Females with addled or infertile eggs took longer for the TFT ($\bar{x} = 5.2$ days, SD = 2.0, $n = 3$) than females with chicks that hatched ($\bar{x} = 2.8$ days, SD = 1.5, $n = 20$) ($t = 2.42$, df = 21, $P < 0.05$). The TFT of the latter varied according to the sum of the time taken for the FFT and SFT ($r = -0.48$, $P < 0.05$, $n = 20$), but not according to the length of the SFT alone ($r = 0.21$, $P > 0.3$, $n = 20$).

In 15 other pairs, 2 had reversed incubation routines (where the male took the FFT), 3 lost their entire clutch in the 9 November storm (the eggs were blown from the nest), 2 had their eggs broken or lost through fighting, and 8 lost their clutch (i.e. at least the remaining egg, if one had already been lost to other causes) because one of the pair failed to return from a foraging trip before its partner deserted. In only 1 desertion did the late mate never return to the colony. In 7 other instances the foraging bird was away for longer ($\bar{x} = 4.7$ days, SD = 3.6, $n = 7$) than the mean foraging-trip time (Table 1) and arrived at the colony an average of 2.5 days (SD = 1.6, $n = 7$) after its mate had deserted.

Durations of the FFT ($\bar{x} = 17.8$ days, SD = 3.0, $n = 5$) and SFT ($\bar{x} = 13.2$ days, SD = 2.2, $n = 5$) for the control birds (the nests of the other two control birds were lost to desertion) did not differ significantly from the foraging-trip times for birds in the study colony (Table 1) (FFT: $t = 0.73$, df = 26, $P > 0.4$; SFT: $t = 0.12$, df = 26, $P > 0.9$). Hatching success was similar in the study (0.86 chicks/occupied nest) and control colonies (0.88 chicks/occupied nest, SD = 0.31, $n = 9$ colonies).

Mate choice.—Fifty-six of the 76 birds that bred in the study colony in 1984–1985 returned to
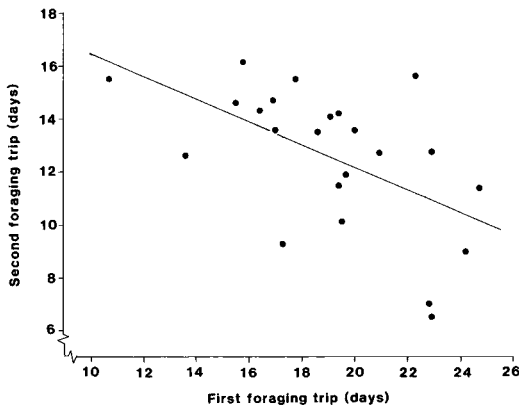
Fig. 1. Durations of the first foraging trip (taken by the female) and the second foraging trip (taken by the male) for pairs of Adélie Penguins ($n = 23$) that successfully coordinated their incubation routine ($y = -0.43x + 20.79$).
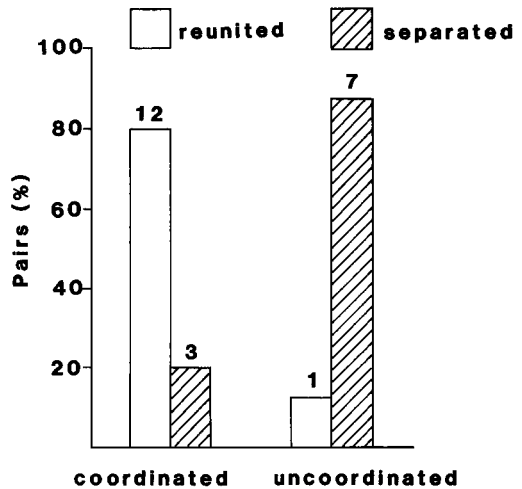

Fig. 2. Percentages of pairs of Adélie Penguins, where both partners returned to the rookery, that reunited or separated depending on whether they had successfully coordinated their incubation routine (i.e. completed the FFT to TFT) the previous season. Numbers of pairs are given above the bars.

the study colony ($n = 55$) or to an adjacent colony ($n = 1$) in the 1985–1986 breeding season. Thirty-four (15 pairs and 4 individuals whose mates did not return in 1985–1986) had been in pairs that successfully completed the FFT to TFT the previous season, while 22 (8 pairs, 5 individuals, and 1 whose 1985–1986 mate could not be determined) were from pairs that failed to complete the FFT to TFT.

Where both partners from the previous season returned, 43.5% changed mates. Pairs that had successfully coordinated nest relief were likely to reunite; those that did not complete the FFT to TFT were likely to separate ($\chi^2 = 7.12$, df = 1, $P < 0.01$) (Fig. 2).

The duration of female foraging trips was consistent between seasons. Those that took the longest FFTs in 1984–1985 tended to take the longest FFTs in 1985–1986 ($r = 0.54$, $P = 0.05$, 1-tailed test, $n = 10$). Complete SFTs were available from both seasons for only a few males ($r = 0.50$, $P = 0.19$, 1-tailed test, $n = 5$).

Retention of nest sites was also related to whether birds had successfully coordinated their incubation routine the previous year. Of coordinated pairs that reunited, 9 (75%) occupied their former nest site and 3 moved an average of only 1.3 nest sites from their old nest (range = 1–2, $n = 3$). Birds that changed mates were significantly more likely to retain their nest site if they had completed the FFT to TFT the previous season (75%, $n = 8$; 2 separated birds did not breed) than individuals unsuccessful at coordinating nest relief (19%, $n = 16$; 2 separated

birds and another whose mate failed to return did not breed) ($\chi^2 = 5.00$, df = 1, $P < 0.05$). Of the latter, females moved to nest sites significantly farther from their old nests ($\bar{x} = 2.3$ nest sites, SD = 1.0, $n = 7$; 1 changed colonies) than did males ($\bar{x} = 0.8$ nest sites, SD = 0.7, $n = 8$) (Mann-Whitney U-test, $U = 77.5$, $P < 0.05$).

DISCUSSION

The durations of foraging trips were known for each pair of Adélie Penguins in 1984–1985. Pairs of Adélie Penguins that successfully coordinated their incubation routine displayed a complementarity in their periods away from the nest. The durations of the second foraging trip taken by the male and the third foraging trip taken by the female were not predicted by time spent fasting (i.e. incubating), but were consistent with the time remaining to the hatching of the chicks. Nearly all desertions resulted from partners failing to coordinate their incubation routine, and not from the death of the foraging partner. The time taken from the beginning of the first to the end of the third foraging trip for pairs was almost exactly equivalent to the incubation period (Penney 1968).

The complementarity of foraging-trip durations resulted, at least in part, from the assortative effects of mate choice. Mates with com-

plementary foraging trips were retained, while those without were not. Penney (1968) and Spurr (1972) reported average annual separation rates for Adélie Penguins of only 16%. By contrast, in banded Adélie Penguins studied over 14 breeding seasons, Ainley et al. (1983) found a mean separation rate of 50.8% for pairs where both partners returned to the rookery the next season. My results are similar. This level of mate retention by Adélie Penguins is the lowest recorded for penguins and is among the lowest for any bird (Rowley 1983). Asynchronous return of partners or limited reinforcement of the pair bond may explain the low level of mate retention in Adélie Penguins.

Penney (1968), Spurr (1972, 1975), and Ainley et al. (1983) attributed separation in Adélie Penguins to the asynchronous arrival of pairs at the rookery at the start of the breeding season. Asynchronous arrival of previous partners is the major cause of separation in the Black-legged Kittiwake (Coulson and Thomas 1983). To explain the observations in this study, penguins that failed to coordinate their incubation routine would have to have been more asynchronous in their arrival at the rookery next season than birds that successfully coordinated incubation.

The degree of reinforcement of the pair bond may determine the likelihood of mate retention (Rowley 1983). For pairs that do not complete incubation there is little opportunity for pair-bond reinforcement. Daily nest relief during the guard stage of chick rearing (Penney 1968, Davis 1982a) provides repeated reinforcement of that bond (Müller-Schwarze and Müller-Schwarze 1980).

The low levels of mate retention in Adélie Penguins at first seem incongruous given that coordination of nest relief is crucial to their breeding success. In colonial seabirds, mate retention increases breeding success primarily through improved parental performance (Ollason and Dunnett 1986). Evidence for such an effect in Adélie Penguins is equivocal (Penney 1968, Spurr 1975, Ainley et al. 1983). Annual mortality is high for breeding Adélie Penguins, and an average adult has only a few seasons in which to breed (Ainley and DeMaster 1980). To be successful, breeding must be initiated within approximately 2 weeks (Davis and McCaffrey 1986). The cost of waiting for a previous mate to return, and perhaps missing a breeding opportunity, probably would exceed any benefit

from improved parental performance (e.g. better coordination of nest relief) through retaining the mate. Only when previous partners arrive synchronously at the colony the following season might an advantage to reuniting be realized.

Foraging-trip duration and the likelihood of mate retention possibly are not influenced by the timing abilities of the penguins. I found tentative evidence that individual females, and perhaps males, are consistent in the relative durations of their foraging trips from one season to the next. Such consistency could result from individual differences in foraging ability (Ainley and Schlatter 1972). The apparent adjustment of the third foraging trip to the incubation period need not result from females measuring the time since laying, but could be a response to a more proximate stimulus, such as chicks peeping inside their eggs just before they hatch. Females with addled or infertile eggs took longer on the third foraging trip. If individual foraging times were relatively fixed and not subject to adjustment by the bird, retaining a mate with incompatible foraging patterns would probably lead to failure again. Separation should then be advantageous irrespective of how synchronously partners arrive at the rookery the next season.

For some species of birds mate retention may be simply a product of nest-site fidelity (Morse and Kress 1984, Cuthbert 1985). In Adélie Penguins mate retention and nest-site fidelity are largely coincidental. Penguins from pairs successful at coordinating incubation tend to return to their previous nest, while unsuccessful birds are likely to change both mates and nest sites. Yet most remain near to their old nests. Fidelity to the site may keep them in the area, and the asynchronous return of their partners may cause them to change mates.

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