DISPLAY RATE AND SPEED OF NEST RELIEF IN ANTARCTIC PYGOSCELID PENGUINS

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ABSTRACT.—The three species of the genus *Pygoscelis, P. adeliae* (Adélie Penguin), *P. antarctica* (Chinstrap Penguin), and *P. papua* (Gentoo Penguin) perform an elaborate Nest Relief Ceremony (NRC) upon one mate's return to the nest. The NRC consists of a number of displays, each of which is performed one or several times. The most conspicuous displays during NRC are the Loud Mutual Display (LMD) and Quiet Mutual Display (QMD) in *P. adeliae* and *P. antarctica,* and their morphologically different functional equivalents in *P. papua,* the "donkey call" (LMD) and "bow-gape-hiss" (BGH). The displays whose repetition rate is negatively correlated with the time elapsed between arrival of the mate and actual changeover are the LMD in *P. adeliae,* "circling" in *P. antarctica,* and BGH in *P. papua.* *Received 17 December 1979, accepted 6 June 1980.*

NEST relief ceremonies (NRC) have been described for many avian species, notably aquatic birds such as herons, pelicans, penguins (Armstrong 1947, Smith 1977), or albatrosses (Lefebvre 1977), or in doves (Heer 1975). Such "formalized interactions" (Smith 1977) often depend on ambivalence, i.e. behavior involving conflict (Hinde 1970). In waterfowl, species with shared incubation have a nest relief ceremony that is most elaborate in the colonially breeding Black Swan (*Cygnus atratus*) (Kear 1970). Three functions ascribed to NRCs in general are appeasement (Lorenz 1938), mate and nest-site recognition, and facilitating nest relief in the mate, the latter described as "stimulating the sentinel to vacate his (or her) post and to make way for the other" (Armstrong 1947).

The genus *Pygoscelis* comprises the Adélie Penguin (*P. adeliae*), the Chinstrap Penguin (*P. antarctica*), and the Gentoo Penguin, (*P. papua*). The Adélie Penguin is distributed circumpolarly in continental Antarctica and breeds most southerly. The Gentoo Penguin is the most northerly species and occurs on subantarctic islands from the Falkland Islands (52°S, 60°W) to Macquarie Island (55°S, 160°E). The Chinstrap Penguin is most restricted in its longitudinal distribution, breeding on the Antarctic Peninsula and islands in the South Atlantic Ocean. The three species overlap in the area of the Antarctic Peninsula (55°–65°S), but segregate by species in pure colonies where they share the same rookeries.

The displays of the Adélie Penguin have been described (Sladen 1958, Sapin-Jaloustre 1960, Spurr 1975) and their motivation analyzed (Ainley 1975), while the displays of the Gentoo (Bagshawe 1938, van Zinderen Bakker 1971) and Chinstrap (Sladen 1955) penguins have been described in only a qualitative fashion. Individual recognition by vocalizations has been demonstrated for the Adélie Penguin (Penney 1968).

The more closely related Adélie and Chinstrap penguins show the same displays in slightly different forms during nest relief. These are the "loud mutual display" (LMD), in which both birds stand and wave their necks back and forth while uttering a loud cackling with open bill; the "quiet mutual display" (QMD), in which both birds wave their necks back and forth and utter a soft humming sound with closed bill (see Fig. 1); and "circling," in which one bird walks around the rim of the nest while nodding with its head. The bird may circle from one step to a full round

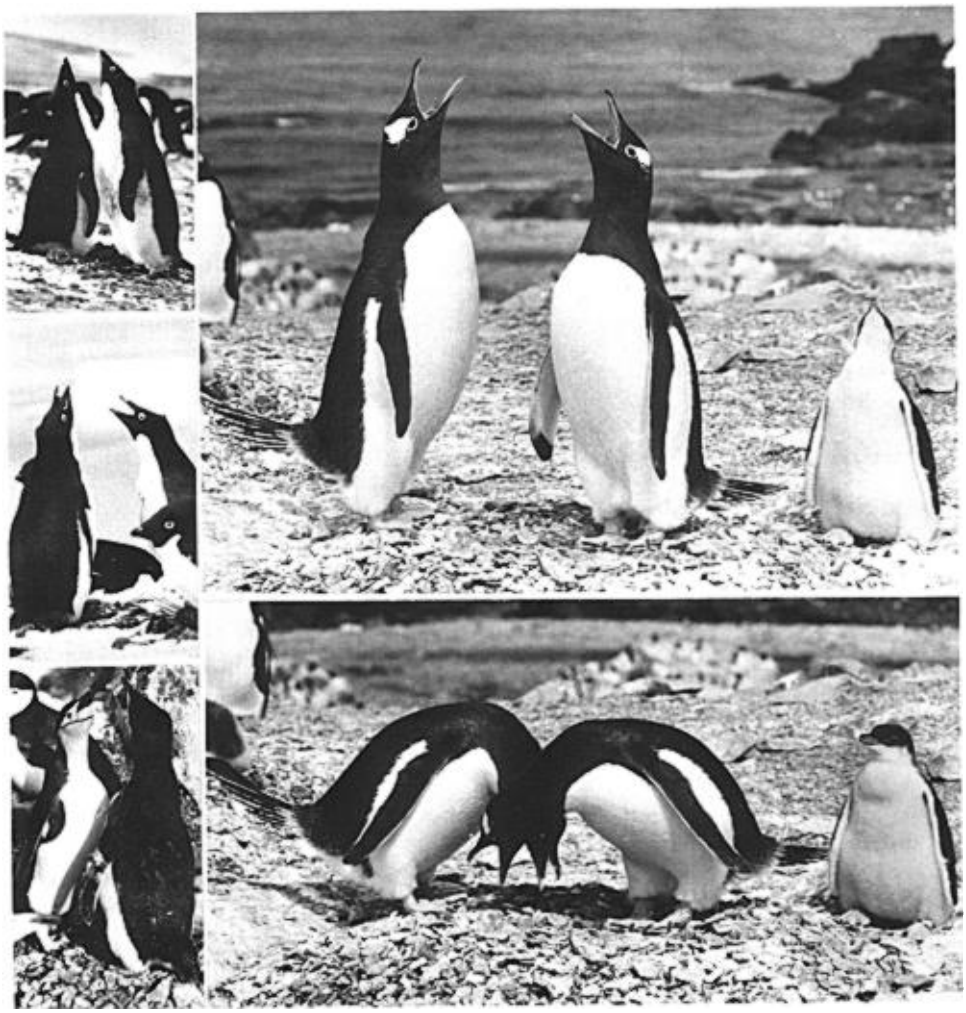

Fig. 1. Clockwise from upper right: Loud Mutual Display (LMD) in Gentoo Penguin (note the participating chick), Bow-Gape-Hiss (BGH) in Gentoo, LMD in Chinstrap Penguin, LMD in Adélie Penguin, and Quiet Mutual Display (QMD) in Adélie Penguin.

around the nest. The Gentoo Penguin's version of the LMD lacks the lateral neck movements, and the sound uttered resembles the braying of a donkey. The second main display of the Gentoo is the "bow-gape-hiss" (BGH), in which the bird bends down to the nest, opens it bill showing the bright red lining, and hisses (Fig. 1). This movement is derived from nest-building behavior, as the Gentoo may deposit a pebble on the nest and then open its bill and hiss.

The functions ascribed to the LMD in the Adélie Penguin are personal recognition (Penney 1968), sexual appeasement and reducing the probability of attack (Spurr 1975), and expression of hesitance to locomote (Ainley 1975). Sladen (1958) suggested three possible functions of the Adélie's LMD: "incipient threat and an appeasement ceremony (i.e. basically aggressive)," "a greeting ceremony," or "a confirmation."

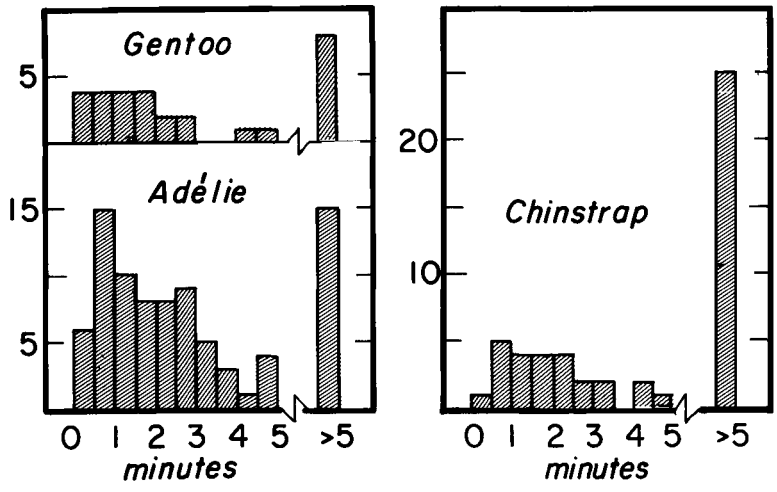

Fig. 2. Frequency distributions of Relief Times (in min) in the three penguin species. Number of observations is given on the ordinate.

These three behavioral contexts overlap, and any display can have more than one function. Roberts (1940) postulated an appeasement function for the Gentoo's BGH.

Here we report correlations between the rates of these displays and the lag until nest relief occurs (Relief Time). The displays used to indicate readiness to switch roles at the nest differ among the three species.

Methods

We recorded 100 NRCs of Adélie Penguins tending chicks ("guard stage") between 24 December 1970 and 6 January 1971 at Cape Crozier in the Ross Sea (77°31'S, 169°23'E), and 31 NRCs during incubation (4–6 December 1971) on Torgersen Island, off the Antarctic Peninsula (64°46'S, 64°05'W). Fifty NRCs were recorded for the Chinstrap Penguin on Nelson Island in the South Shetlands (62°19'S, 50°15'W) between 2 January and 15 January 1972. We recorded 50 NRCs for the Gentoo Penguin between 29 December 1971 and 7 January 1972. Both species bred at the same site, and were observed during the guard stage. Each pair was observed only once.

We recorded NRCs for 5 min from the time a returning bird approached its nest and mate. All behavior patterns performed by the arriving bird, by the bird on the nest, and by both individuals jointly were recorded on prepared data sheets. After each 5-min observation, one or (when the first bird was difficult to sex) both birds of the pair were caught with a net and sexed by means of a cloacoscope. The exact time that a bird had spent on the nest before being relieved was not known. Adélie Penguins relieve one another about three times during the 37 days of incubation and about once a day after the chicks have hatched (Sladen 1958, Penney 1968).

Results

The frequency distributions of the three species' relief times are shown in Fig. 2. Relief time averages 2.63 min in the Adélie Penguin and the arriving bird starts the LMD regardless of its sex. They average 7.9 LMDs (range 1–18) before nest relief during incubation and 6.7 during the guard stage (2–15). The QMD is less frequent: 0.29 (0–4) during incubation and 0.61 (0–8) during guard stage. The number of LMDs per minute is negatively correlated with the nest relief time: 5 LMDs per min precede nest reliefs that take place 1–3 min after arrival of the mate, while 1 display per min is usually followed by a nest relief after 5 min or longer (Fig. 3A).

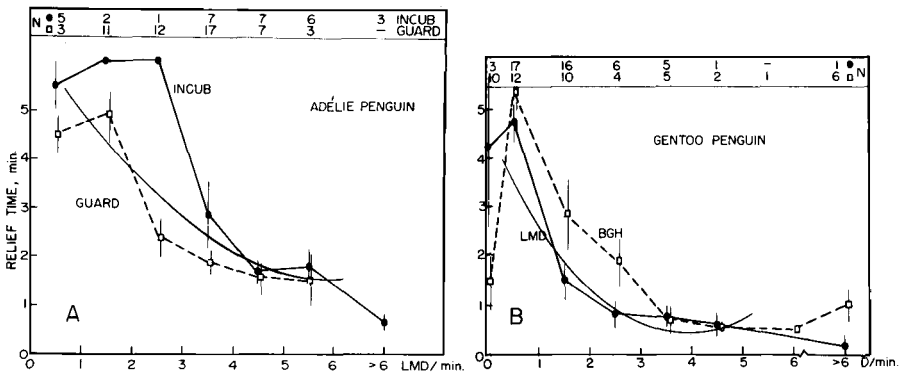

Fig. 3. A. Rate of loud mutual display (LMD/min) between arrival of mate and relief in relation to relief time in Adélie Penguins. Dots = incubation period (Torgersen Island); squares = guard stage (Cape Crozier); N = number of nest reliefs analyzed. Vertical lines indicate standard error of mean. The solid curve indicates the values expected from a multiple regression analysis (see text). B. Rate of loud mutual displays (LMD/min) and bow-gape-hiss (BGH/min) (D/min = displays per min) in relation to relief time in Gentoo Penguins. All data from guard stage at Nelson Island; N = number of reliefs analyzed; solid curve as in A.

The number of LMDs during the first 30 s after arrival of the mate is predictive of the relief time (Fig. 4A). During incubation at Torgersen Island (T), the bivariate correlation coefficient $r_T = -0.461$ ($P = 0.005$), and during guard stage at Cape Crozier (C), $r_C = -0.390$ ($P < 0.005$). The difference between r_T and r_C is not significant. In the Adélie Penguin the rates of QMD, circling, nestbuilding, or preening are not correlated with relief time. Nest building occurred only 4 times during 50 reliefs, and preening 3 times. Stepwise multiple regression analysis for relief time (RT, variable 1), LMD (2), and QMD (3) during the entire time until relief yields the partial correlation coefficients $r_{12.3} = -0.645$, $r_{13.2} = 0.357$, and $r_{23.1} = 0.001$. None of these values is significant at $P < 0.05$. This shows that more precise information is exchanged during the initial 30 s than during the remainder of the relief time (multiple $R = 0.788$; $R^2 = 0.544$). The regression equation RT = 4.742 − 0.660 LMD + 1.865 QMD reflects the trend shown in Fig. 3A. Because only the regression coefficient for LMD is significant ($P < 0.02$), the equation RT = 6.515 − 1.676 LMD + 0.148 LMD^2 fits the data better (shown in Fig. 3A).

Chinstrap Penguins relieve each other after 3.63 min on the average (if times longer than 5 min are arbitrarily counted as 5.5 min). They average only 1.38 LMDs (range 0–4) per NRC. The LMDs occur at the beginning when the birds meet, can be started by either sex, and the nest bird and arriving bird display equally often. The QMD is more frequent than in the Adélies ($\bar{x} = 4.88$, range 0–17) and is more often started by the bird at the nest ($P < 0.001$) than by the arrival. Only females show the QMD in response to the mate's feeding the young ($n = 17$; $P < 0.005$). Circling is the Chinstrap's only display whose rate is correlated with relief time. A high frequency of circling during the first minute is followed by a fast relief ($r = -0.410$, $P < 0.005$). The intensity of circling, measured in angular degrees, shows no correlation with relief time. The arriving bird circled before relief in 28 of 29 cases. The nest bird circled in 24% of all cases, before and after relief. Not correlated with relief time were the number of LMDs ($r = -0.034$, NS) and the frequency of bowing ($r = -0.067$, NS) during the first 30 s (Fig. 4B).

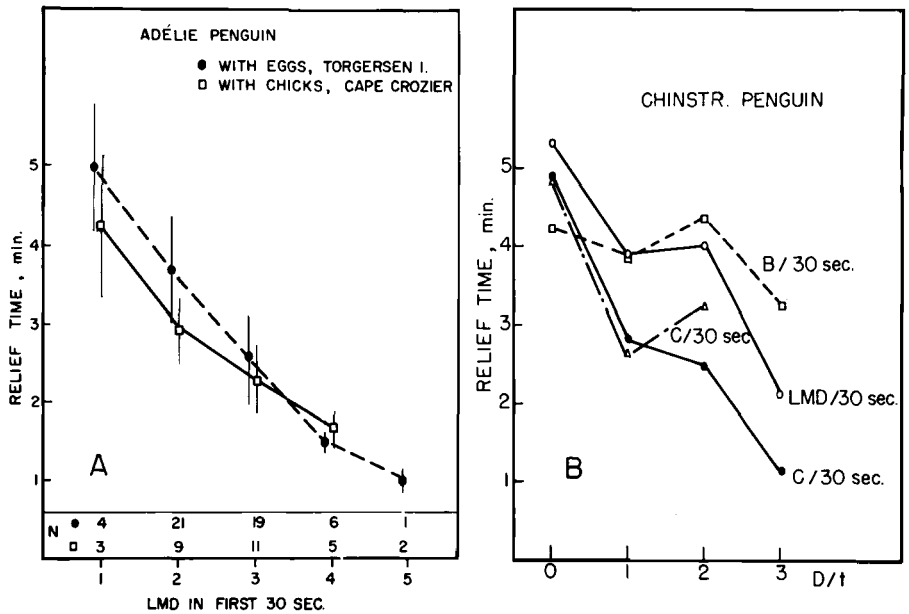

Fig. 4. A. Number of LMDs in first 30 s after arrival of mate in relation to relief time in Adélie Penguins. Dots = incubation period, Torgersen Island; squares = guard stage, Cape Crozier. B. Frequency of LMD, bowing (B), and circling (C) during the first 30 s and C during first min in relation to relief time in Chinstrap Penguins. The abscissa gives displays per time unit (D/t) of 30 or 60 s.

Stepwise multiple correlation was performed for Chinstrap Penguin relief times (1), QMDs (2), and Circlings (3) during the first 30 s and LMD (4) during the first 60 s. The partial correlation coefficients are: $r_{13.24} = -0.3150$; $r_{14.23} = -0.2940$; $r_{23.14} = -0.2887$; $r_{34.12} = -0.0623$; and $r_{12.34} = 0.0122$. The better correlation of relief time with LMD and circling is also shown in Fig. 4B. The corresponding bivariate correlation coefficients are very similar: $r_{13} = -0.3263$; $r_{14} = -0.2863$; $r_{23} = -0.3077$; $r_{34} = -0.0267$; and $r_{12} = 0.104$. The regression equation for the Chinstrap is: RT = 5.253 − 0.890 LMD − 0.575 C (the regression coefficient for QMD was not significantly different from zero); $R^2 = 0.184$.

Relief time averages 2.4 min in the Gentoo Penguin. The nest bird starts the LMD most often ($P < 0.01$) regardless of the sex of the bird, and it occurs usually only once or twice when the mates meet ($\bar{x} = 1.92$, range 0–8). The BGH is more frequent ($\bar{x} = 3.22$, range 0–13) than the LMD and is started most often by the arriving bird ($P < 0.001$). A short nest relief ceremony results when the arriving bird gives a rapid sequence of BGH displays. Changeover occurs within 1 min or less after 4–5 displays per min; an arrival-relief interval of 2 min to over 5 min is correlated with 0.5 displays per min (Fig. 3B). If the bird at the nest joins in the BGH of the arriving bird, time from arrival to nest exchange is shortened: relief time was shorter than 200 s in 78% of the cases in which over 50% of the arrival's BGH led to mutual BGH (44% of those in which under 50% led to mutual BGH). ($P = 0.025$). Rates of other behaviors were not correlated with relief time. The partial correlation coefficient for LMD (1) and BGH (2) is $r_{12.3} = 0.452$, that for BGH (2) and Relief Time (3) $r_{23.1} = -0.412$, and that for LMD (1) and Relief Time (3) $r_{13.2} = -0.134$. The regression equation RT = 5.1 − 3.051 LMD + 0.615 LMD^2 − 0.034 LM^3 describes the relationships for 1–5 displays per min (Fig. 3B).

When returning to their nests after having been captured and sexed, males showed better orientational ability. Males headed straight for the nest in 13 of 15 cases, while females did so in only 1 out of 8 cases ($P < 0.005$). Females often headed for the sea or approached strange nests where they were attacked and became more "confused."

DISCUSSION

To our knowledge this is the first demonstration of a correlation between the rate of an avian display and the time of nest relief. Three communicatory implications can be distinguished. First, the arriving bird indicates its readiness to relieve the mate by its display intensity, measured as rate of repetition. Second, the nest bird in turn may indicate its readiness to leave the nest by its displays, either spontaneously, as in doves (Heer 1975), or in response to the arriving bird's behavior, resulting in mutual displays. Third, in addition to announcing its already existing readiness, each bird may stimulate the behavior of the other and accelerate the relief by synchronization of the pair. We have demonstrated the first two effects, but the stimulatory function of the displays must be analyzed by experimental techniques.

The need for a precisely synchronized nest relief that minimizes the time of exposure of eggs or chicks is particularly great in Antarctic penguins for two reasons: exposed eggs or chicks may be chilled, and they may be preyed upon by South Polar Skuas (*Catharacta maccormicki*) within a few seconds. By comparison, other birds leave their eggs exposed for considerably longer times. For example, successfully breeding female Pink-footed Geese (*Anser brachyrhynchus*) in Iceland were absent from the nest 3.8% of the time on the average, broken down into several episodes daily (Inglis 1977). This is about 1,000 times longer than the estimated 3 s that the Adélie Penguin's eggs are exposed during a nest relief. Smith (1969) stressed that the response to a message has to meet the needs of both the recipient and the communicator. In the case of nest relief, communication between the mates serves to protect their investment in a third party, their eggs or chicks.

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