A QUANTITATIVE ANALYSIS OF THE INCUBATION BEHAVIOR OF THE ADÉLIE PENGUIN

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ABSTRACT.—The incubation period of the Adélie Penguin was studied quantitatively to determine the behavioral requirements for successful reproduction. Incubation was divided into early, middle, and late periods to facilitate comparison between sexes and to evaluate activity in relation to stages of incubation.

Analysis of time-lapse photo sequences showed that prone postures accounted for 87 to 95% of the nest time from clutch completion to hatching. Upright postures were most often comfort movements and were more frequent during the prelaying, laying, and late (hatching) periods than in early and middle incubation.

Intensity of incubation was measured by the time an incubating bird spent in prone and upright positions. Prone postures were considered more intense. Intensity increased rapidly following clutch completion. Attentive periods increased in duration and decreased in number per day as the laying phase was completed. Incubation intensity remained stable from clutch completion to hatching. An increase in upright restless activity during hatching probably was a result of chick feeding and vocalization and response to the movement on nonincubating birds passing the nest. No statistical difference in incubation intensity between sexes was found.

A diurnal rhythm of upright restless movements during incubation was shown. There was considerable variation in restlessness from day to day and between individuals, but when all birds were grouped, a cycle of activity emerged. Peak restless activity occurred at 1100 G.M.T. Two external factors, ambient air temperature and light intensity, were compared with upright restlessness. Light intensity and activity showed nearly identical cycles. Ambient air temperature showed no obvious relationship to restlessness. Social activity may influence restlessness during incubation.

Egg temperatures were measured to determine incubation postures functional to heat maintenance and also to learn of changes during incubation. Collation of incubation events observed from a blind and recorded egg temperatures showed that eggs chilled rapidly when birds stood upright. A buildup in egg temperature from incubation day 12 to a maximum on day 21 occurred. A general trend of decreased upright restless movement corresponded to the buildup in egg temperatures and is probably responsible for it. Higher, more stable egg temperatures were shown for the middle period of incubation. Toward hatching egg temperatures fluctuated, but they did not drop drastically until after hatching.—*Department of Zoology and Entomology, Iowa State University, Ames, Iowa 50011. Present address: U.S. Fish and Wildlife Service, 813 D Street, Anchorage, Alaska 99501.* Accepted 15 December 1975.

ADÉLIE PENGUINS (*Pygoscelis adeliae*) have adapted to the harsh antarctic environment characterized by low temperatures, high winds, a short austral summer, and limited nesting places. These conditions influence the timing of the breeding season and the reproductive strategy of the pair. Effective timing and organization of events by both sexes is essential if chicks are to reach maturity while the sea is unfrozen.

Time from arrival at the rookery to appearance of the first egg is about 10 days (Stonehouse 1963), and over 90% of laying is completed within a 12-day period (Penney 1968). Laying periods for penguins found at lower latitudes are longer (Stonehouse 1970). Richdale (1941b) reported a 5-month egg-laying span for the Little Blue Penguin (*Eudyptula minor*) of temperate New Zealand. The 34- to 37-day incubation period of the Adélie Penguin is short compared to the 40 to 50 days in the Yellow-eyed Penguin (*Megadyptes antipodes*) (Richdale 1941a) of New Zealand.

Both sexes occupy the nest during the laying period. Following clutch completion, the females depart for the sea to feed, while the males almost always assume the first incubation watch (Sladen 1958). Incubating birds rarely leave the nest as so doing would mean the loss of its contents to freezing temperatures or the South Polar Skua (*Catharacta maccormicki*).

Drent (1970) showed that a number of gradual changes, such as increased attentiveness and aggression, take place between clutch completion and the first signs of pipping in the Herring Gull (*Larus argentatus*). Other studies of birds nesting in temperate climates have demonstrated similar changes during incubation (Kendeigh 1952, Prescott 1964). Little is known of possible changes that may occur during the course of incubation or of variations in behavior among incubating penguins that nest in more rigorous climates.

Müller-Schwarze (1968) suggested a circadian rhythm in some activities of Adélie Penguins during incubation, but Yeates (1971), working at a more southerly Adélie rookery, found no such pattern. Eklund and Charlton (1959) recorded egg temperatures of incubating Adélie Penguins, but did not study the relationship of the birds' positions on the nest to egg temperatures. Weinrich (1972) showed that Adélie Penguin embryonic development was accelerated at higher incubation temperatures. A trend of increased broodiness demonstrated by Fredrickson and Weller (1972) may affect egg temperature and thus the rate of development.

Although some postures and aspects of the Adélie Penguin's incubation process have been studied, their behavior throughout incubation has not been analyzed quantitatively. The objectives of this study were: (1) to quantify the time allocated to various incubation activities by sex and by day of incubation, (2) to determine egg temperatures and evaluate the influence of incubation postures on egg temperatures, and (3) to assess diel rhythm with minimal light changes.

Procedures

The study was conducted at Cape Hallett (72° 19′ S, 170° 13′ E), Antarctica during the austral summers of 1969–71. The Adélie Penguin rookery contains about 48,045 breeding pairs (Fredrickson pers. comm.) and is located on an ice-free peninsula of about 40 ha. The main study colony (B-75 of Reid 1964) contained about 30 breeding pairs of Adélie Penguins. A heated hut for observations also housed two time-lapse movie cameras and up to four thermographs. Observation periods ranged from 2 to 5.5 h.

Banding and marking.—To identify individuals, birds were banded during 1969–70 with aluminum flipper bands designed by Sladen et al. (1968). Age of the banded incubating birds was estimated to be greater than 4 years based on evidence that Adélies seldom breed before this age (LeResche and Sladen 1970). Several birds in the colony used in this study were banded as breeding adults by D. Thompson in 1967–68, so they were a minimum of 6 years old in 1969–70. The same colony and many of the same birds were studied in the following two summers.

Sex of the birds was determined by observing copulatory position (Sladen 1958, Penney 1968) in 1969–70 and was verified for returning birds in 1970–71 and 1971–72. The sex of incubating birds was denoted by spray-painting a black band across the chest of males and lower sides of females so that photographs would record sex as well as postures of birds.

Time-lapse photography.—The use of time-lapse photography proved accurate for recording events of several pairs of incubating birds simultaneously (Weller and Derksen 1972). Accuracy depended largely on camera timer interval and the camera's ability to operate for several days without a battery change. I used 1-minute interval exposures because film and battery replacement was necessary only every 60 h.

Behavior of five pairs of Adélies during and prior to incubation was continuously recorded with two 8-mm Braun-Nizo S-80 cameras in 1969–70. Five and two pairs of birds were photographed with Nizo cameras from the observation hut in 1970–71 and 1971–72, respectively. Some 108,000 individual frames (more than 1,500 ft) of plus-X black-and-white Super 8 film were analyzed during the study.

Egg temperature.—A plastic, hollow "Easter egg" (45 × 63 mm) of the kind used by Fredrickson and Weller (1972) was fitted with a thermistor probe and substituted for one of the two natural eggs in one Adélie Penguin nest. The egg was anchored by running the probe lead wire under the stones of the nest. Although movement of the egg was restricted by the lead wire, the incubating bird could turn it partially. Temperatures of the plastic egg were monitored continuously from 2 to 20 December 1970, with a VirTronics Model 56-TR thermistor temperature recorder.

Except for initial egg pecking by some incubating birds, behavior was not visibly altered by the anchored plastic egg. Positions of the experimental thermistor egg and the remaining natural egg were changed by the brooding bird during the 19 days of recording.

An Adélie egg also was fitted with a thermistor probe to determine the temperature and heat-holding capacity differentials between natural and plastic eggs. The probe was inserted through a small hole drilled in the large end of the egg and sealed with epoxy glue. A continuous 27-hour temperature record was obtained before the egg broke.

Methods of recording egg temperatures were similar in 1971–72 except that one pair of birds was photographed at 1-min intervals and the plastic egg was monitored for temperatures simultaneously for the entire incubation period. Correlation of filmed events and egg temperatures provided a method of determining which events (preening, displays, etc.) influenced the temperature of the egg.

Data analysis.—Time-lapse films were analyzed frame by frame with the aid of a Kodak MFS-8 Super 8 projector. Forty-five events (postures, displays, etc.) were assigned two-digit codes (01 to 45) for computer analysis. Each event was recorded on an IBM coding sheet, and events both on and off the nest were tabulated. Film sequences during the few minute disturbances of changing film and winding clocks were deleted. The 45 events were grouped in eight categories:

(1) Resting and sleeping—resting includes postures with open eyes in which the bird was not visibly alert. Sleeping postures occurred with the bill on or under either flipper, and the more frequent posture in which the bill points forward.

(2) Agonistic and territory defense—agonistic includes postures characterized by one or all of the following: (a) open eyes with sclerae often exposed, (b) erect occipital crest feathers, and (c) head elevated from the more horizontal resting and sleeping postures. Territorial defense includes threat displays or pecking at adjacent or passing birds, or birds stealing nest stones, and attack and fighting.

(3) Nest-building—time spent moving stones from the perimeter onto the nest or arrangement of stones in the nest.

(4) Comfort movements and preening—includes the head-shake, body-shake, tail-wag, head-scratch, rapid-wing-flap, and both-wings-stretch (Ainley 1974), also excretion.

(5) Sexual displays—included here are displays and postures associated with pair formation and maintenance, such as the ecstatic display, oblique stare bow, and loud and quiet mutual displays (Penney 1968). Copulation also is included here.

(6) Rotations—movement of birds in either direction in the nest with or without the presence of eggs.

(7) Egg-shifting—this includes the time spent turning or changing the relative position of the eggs.

(8) Nest relief—the ceremony before and after the exchange of pairs.

Continuous strip temperature records were cut into three 8-h pieces for each day and mounted on paper for handling ease. An acetate overlay, marked at 5-min intervals, was placed over the strip records to obtain mean daily egg temperatures based on 288 observations per day.

RESULTS

TIME BUDGET

Time budgets (Table 1) for three pairs of birds on nests are based on analysis of about 800 h of time-lapse sequences filmed during the prelaying and incubation periods. The primary comparison is between time spent in prone and upright activities during prelaying, laying, and incubation. Incubation was divided into early, middle, and late periods to facilitate comparison between males (early) and females (middle) and to evaluate activity near hatching (late). Early incubation includes the time from clutch completion and female departure until nest relief at her return. Midincubation is the time from nest relief and male departure until his return to the nest 2 or 3 days before hatching. Because egg temperatures monitored during December 1969 revealed pronounced fluctuations during the final stages of incubation, a third category (late) was created, which here corresponded to the time of the males' second watch.

Prone versus upright.—Most time on the nest was spent in prone positions (Table 1). Birds assumed prone postures from 72 to 95% of the time during prelaying, laying, and incubation. More than twice as much time was spent in upright positions on the nest during the prelaying period (27.8%) compared to the laying period

TABLE 1

TIME BUDGET FOR INCUBATING ADÉLIE PENGUINS

	Proportion of time spent prone					Proportion of time spent upright				
Activity	Pre-laying (–6–0)[1]	Laying (1–5)	Early (6–13)	Middle (19–29)	Late (33–38)	Pre-laying (–6–0)	Laying (1–5)	Early (6–13)	Middle (19–29)	Late (33–38)
Resting and sleeping	50.22	60.84	71.73	82.73	66.09	7.44	1.53	0.01	0.05	0.0
Agonistic and territory defense	8.67	12.56	16.13	11.17	20.13	8.43	5.30	2.53	1.60	6.54
Nest building	0.67	0.35	0.19	0.01	0.09	1.75	0.59	0.10	0.08	0.07
Comfort and preening	0.0	0.0	0.0	0.02	0.0	0.35	0.72	1.23	1.18	0.78
Sexual displays	—	—	—	—	—	1.91	0.52	0.23	0.0	0.06
Rotations	—	—	—	—	—	4.78	3.27	0.85	1.47	1.74
Egg-shifting	—	—	—	—	—	—	0.30	0.16	0.17	0.20
Unknown	12.63	13.47	6.83	1.52	4.27	2.32	0.34	0.01	0.0	0.01
Nest relief	—	—	—	—	—	0.83	0.21	—	—	0.02
Total[2]	72.19	87.22	94.88	95.45	90.58	27.81	12.78	5.12	4.55	9.42

[1] Numbers in parentheses indicate day of incubation.
[2] Sum of identical column headings = 100.00%.

(12.8%) and early, middle, and late incubation. The least amount of time spent in upright positions (5.1 and 4.6%) occurred in early and middle incubation. A slight increase to 9.4% in time spent upright occurred during the late incubation period.

Resting and sleeping.—Prone rest and sleep dominated (50 to 82%) (Table 1), with the least amount (50.2%) occurring during prelaying. Most values for upright rest and sleep for each nesting stage were about 1% of the total time expenditure (range 0.0 to 7.4%). Difference between time spent in prone rest and sleep was statistically significant ($P < 0.005$) from upright rest and sleep.

When prone and upright rest and sleep positions were combined for prelaying, laying, and early, middle, and late incubation, the proportion of time spent resting increased about 10% for each of the first four stages, with a 10% reduction during late incubation. The percent time spent resting in these five stages is statistically different by analysis of variance ($P < 0.005$). As prone rest and sleep increased, upright rest and sleep declined (Table 1). Period-position interaction is statistically significant ($P < 0.005$).

Agonistic and territory defense.—Birds searching for nest stones frequently initiated alertness in nesting birds. Territorial conflicts usually elicited threat postures, as did noise from conflicts in nearby colonies. The cause of agonistic behavior could not always be determined on the time-lapse films.

Upright and prone agonistic postures were the second most important time expenditure (Table 1). Less than half as much time was spent in upright as in prone agonistic positions in all but the prelaying period, which showed nearly equal values. The difference is significant ($P < 0.01$) for the two positions, as is the difference between the five nesting periods ($P < 0.005$).

Interaction between the period and the prone and upright agonistic positions is significant ($P < 0.005$). Although a large drop in percent of time spent in prone agonistic postures occurred in the middle incubation period (Table 1), prelaying, laying, and early incubation determined significance in this analysis.

Nest-building.—Arrangement of nest stones by the incubating bird is accomplished from both upright and prone postures (Table 1), but time spent building in

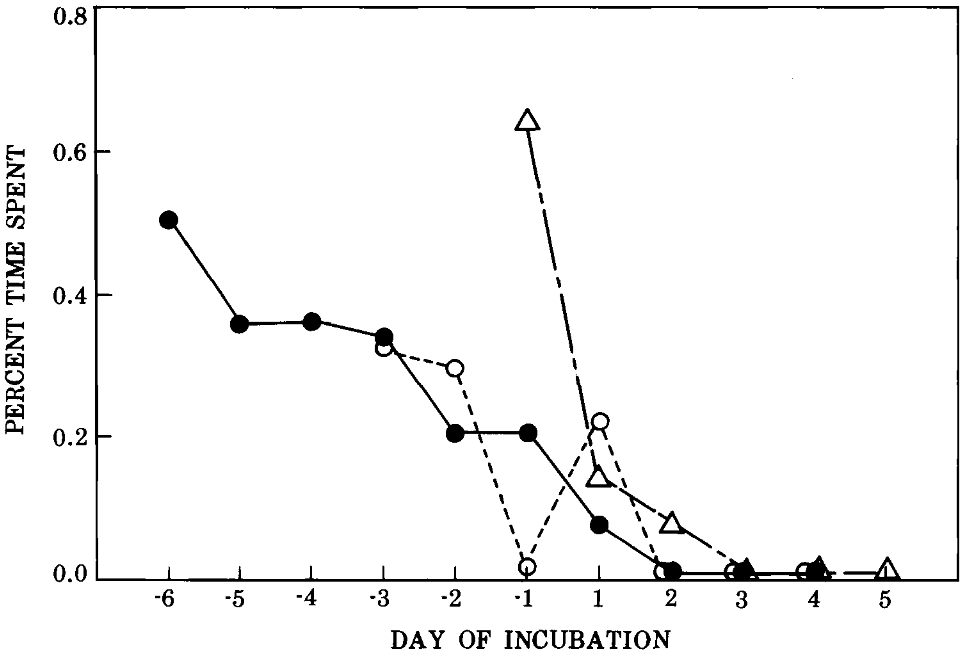

Fig. 1. Frequency of copulation for three pairs of Adélie Penguins.

each position was not statistically different ($P < 0.01$). Combined values for prone and upright nest-building show a significant ($P < 0.005$), progressive decline in such activity during nesting.

Comfort movements and preening.—Comfort movements, such as the both-wings-stretch, body shake, and preening were usually upright postures (Table 1). The time devoted to comfort movements and preening was not significantly different between periods ($P < 0.1$).

Sexual displays.—Sexual displays included in the analysis were the ecstatic display, oblique stare bow, and loud and quiet mutual displays. The oblique stare bow was not easily discernible on film and so was probably alternately included in both the agonistic and sexual displays categories.

As was the case in nest-building, time spent exhibiting sexual displays showed a progressive decline as the season advanced (Table 1). A significant difference ($P < 0.005$) between periods was found by analysis of variance. Male birds spent 0.23% of the total nest time in sexual displays during early incubation, mostly in ecstatic displays. No females exhibited the ecstatic display in film sequences analyzed (Table 1), although one banded incubating female once gave this display. Copulation occurred only during the prelaying and laying period. Figure 1 shows the frequency of copulation for three pair of birds during the prelaying and laying periods determined from 1-min time-lapse films.

Rotation.—Movement in the nest bowl is functional in changing relative position of the eggs, as well as turning the egg(s). The movement is characterized by a hunched posture and shuffling of the feet. One method of egg rearrangement is accomplished by rotating either direction during which the front egg remains between the feet, while the rear egg is momentarily exposed (Fig. 2). The rotation is completed to 180°, and the rear egg has assumed the front position. Rotations also occurred before egg-laying.

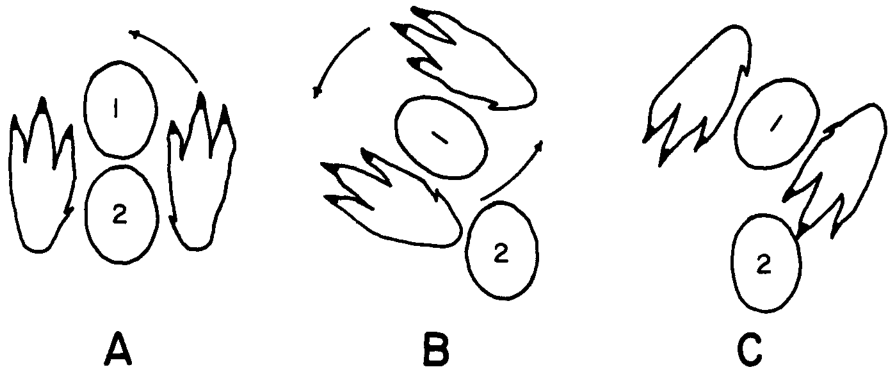

Fig. 2. Position of Adélie Penguin feet during egg rearrangement. Arrows show direction of movement.

Birds spent more time (4.78 and 3.27%) rotating during prelaying and laying periods than during incubation (early = 0.85%, middle = 1.47%, and late = 1.74%) (Table 1). The difference between periods is statistically significant ($P < 0.005$).

Egg-shifting.—In addition to rotating the eggs with the feet, Adélies also use their beaks to turn the eggs. Egg-shifting during the laying period was about double the time spent in any of the other periods ($P < 0.005$). Time spent shifting the egg(s) during various stages of the incubation period was similar (Table 1).

Nest relief.—Nest relief ceremonies were four times as frequent during prelaying (0.8% of the total observation time) as during laying (Table 1).

Males versus females.—Examination of the means of the early (males) and middle (females) incubation periods reveals nearly identical means for resting, nest-building, comfort postures, and preening, and egg-shifting in the upright position (Table 1). Differences between early and middle incubation periods occurred in prone rest and sleep (males = 71.7%, females = 82.7%) and agonistic and territory defense (males = 16.1%, females = 11.2%) categories.

Despite the differences between males and females noted above for various activities, almost identical amounts of time were devoted to all prone (males = 94.9%, females = 95.5%) and all upright (males = 5.1%, females = 4.6%) postures during incubation (Table 1). These figures show males and females provide nearly equal amounts of egg coverage time and suggest similarities in incubation intensity.

Incubation Intensity

The intensity of incubation is based on the amount of time an incubating bird spends in prone rather than upright positions. Incubation in the prone position, with the eggs covered by the brood patch, is considered more intense than upright positions in which the eggs may be only partially covered.

Examples of the buildup in incubation intensity are shown in Fig. 3. Intensity of incubation by both sexes during laying is less than that following laying, as evidenced by the general trend toward less time devoted to upright positions (Fig. 3, Table 1). Time spent on the nest by males also builds up during the laying period (Fig. 3).

Increased incubation intensity associated with laying also is demonstrated by the longer duration and decreased number of attentive periods by both sexes (Table 2). Fewer nest exchanges during the laying period would mean less time spent in upright positions and, consequently, more intense incubation.

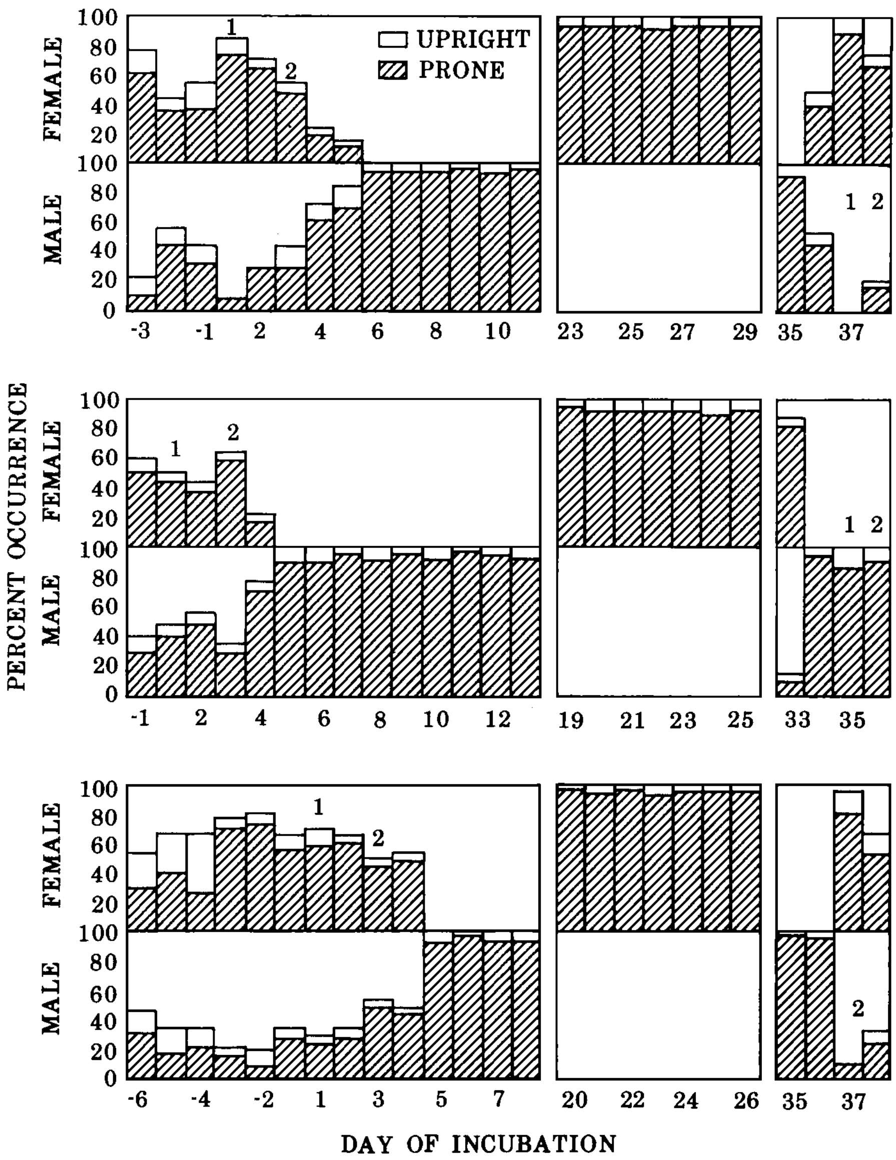

Fig. 3. Incubation schedules at three Adélie Penguin nests. Numbers over bars indicate laying and hatching dates of first and second eggs.

In the period between clutch completion and hatching, the Adélie maintains a relatively constant intensity of incubation (Fig. 3). Fewer restless upright movements would mean longer attentive periods and presumably more even incubation temperature. Males spent 94.9% of the time on the nest in intense prone incubating positions, and females were prone 95.5% of the time during their second watch (Table 1).

During hatching, incubation intensity again decreases, as shown by the increased amount of time devoted to upright restless movements (Fig. 3, Table 1). This decrease may have been due to chick feeding and/or response of the adult to chick vocalizations before hatching.

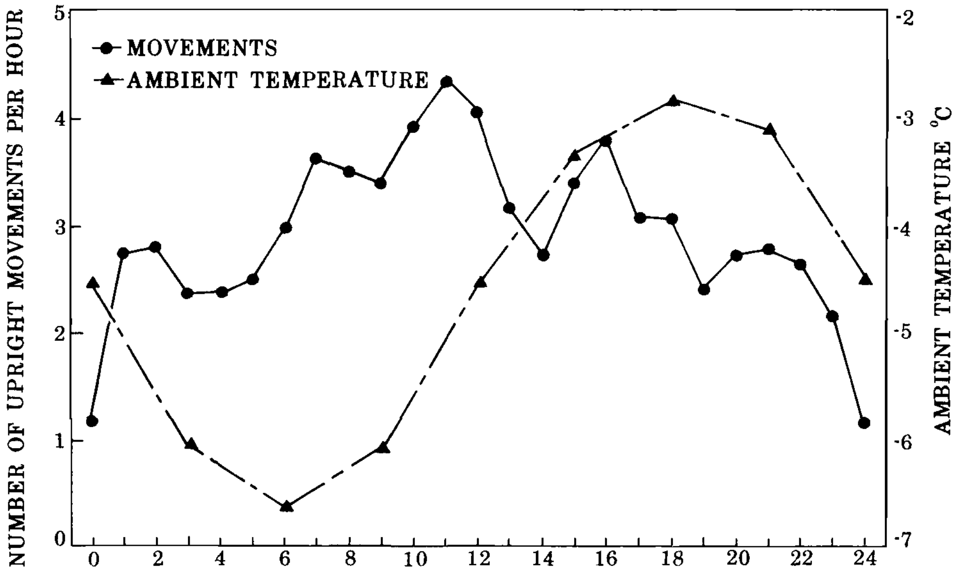

Fig. 4. Diurnal rhythm of incubation in the Adélie Penguin.

Diel Rhythm of Incubation

To quantitate daily incubation rhythm, mean activity of three pairs of birds was plotted for 28 days during the incubation period based on 1-min interval time-lapse films (Fig. 4). Interruptions in prone incubation included upright postures such as: nest-building, preening, comfort movements, stares, fighting, rotations of the incubating bird, and egg-shifting. A plot of the mean ambient temperatures, recorded at 3-h intervals, also is shown for these same days.

Ambient temperature cycle did not seem to be a factor controlling activity during incubation (Fig. 4). Hours of increased upright activity (0900–1100 and 1400–1600) sometimes corresponded with temperature increases and at other times (0300–0700) with temperature declines.

The diurnal rhythm of upright restless activity of incubating Adélies was related to the light cycle. Incubation activity varied from day to day and between individual

TABLE 2
Frequency and Duration of Attentive Periods at One Adélie Penguin Nest

Day of incubation	Number of attentive periods		$\bar{x}$ Duration of attentive periods (min)		Range (min)	
	Male	Female	Male	Female	Male	Female
−6	6	8	69.5	62.5	16–205	25–122
−5	6	8	76.0	120.1	14–117	2–275
−4	5	9	84.4	95.2	25–168	14–324
−3	3	4	63.0	167.5	20–97	27–314
−2	4	5	67.5	233.8	32–125	87–371
−1	5	7	97.6	129.9	17–184	23–245
1	3	3	128.3	307.7	88–168	58–511
2	2	2	363.0	357.0	216–510	298–416
3	2	2	352.0	368.0	335–369	198–538

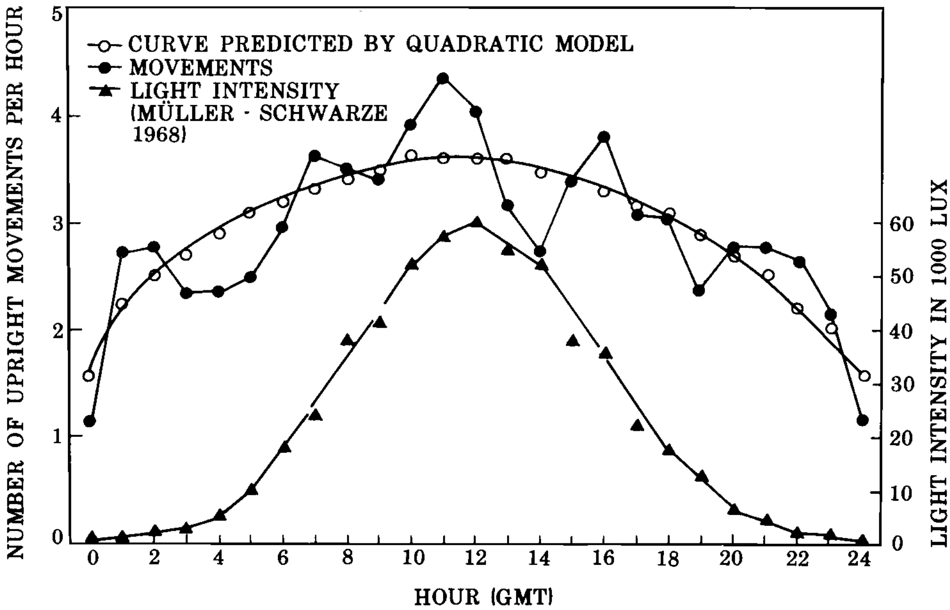

Fig. 5. Relationship of incubation rhythm and light intensity.

birds, but the mean of six birds showed maximum activity at 1100 G.M.T. and minimum activity at 2400 (Fig. 5). Use of a simple quadratic model ($y = b_0 + b_1h + b_2h^2 + e$) to approximate the unknown functional relationship between activity and hour gave the fit shown in Fig. 5. Records of light intensity were not kept in this study, but Müller-Schwarze (1968) reported a diurnal change in light with peak intensity occurring at 1200 for two different time periods (November and January) at Cape Hallett (Fig. 5).

Effect of Behavior on Egg Temperature

Adélie Penguin eggs were not completely covered when the incubating bird assumed upright positions. Time budgets (Table 1) showed more upright activity during the laying and hatching periods. It would seem that exposure associated with upright activity would influence egg temperature and, consequently, trends in temperature during various periods of incubation.

Spellerberg (1969) investigated the cooling effect of the environment at Cape Royds (77°33′S, 166°09′E) on exposed South Polar Skua eggs. He showed that an egg cooled from 32° to 0°C in 14 min (2.3°C/min) at air temperatures of −2.0° to −4.5°C. The ambient temperatures for three austral summers (1963–66) at Cape Royds ranged from −15.0°C in November to 5.0°C in March (Spellerberg 1969). These air temperatures are comparable to those recorded at Cape Hallett in 1969. Cooling rates for penguin and skua eggs may be slightly different because of volume difference, but the influence of antarctic ambient temperatures on egg thermal maintenance is significant to both of these species.

In 1969 a plastic egg with thermistor was placed in a nest for a 17-day period (incubation days 23–39), and in 1971 a plastic egg monitored egg temperatures for 35 days (incubation days 4–39) in a nest continuously filmed for 18 days (incubation

TABLE 3

UPRIGHT RESTLESS MOVEMENTS OF FEMALE ADÉLIE PENGUIN IN RELATION TO TEMPERATURE OF PLASTIC EGG

	Egg in front				Egg in back			
Activity	n	Mean duration (s)	Mean temp. loss (°C)	°C/s	n	Mean duration (s)	Mean temp. loss (°C)	°C/s
Alert to intruder	28	9.3	0.4	0.04	11	15.7	0.5	0.03
Rotation	31	17.3	1.2	0.07	15	19.2	0.8	0.04
Multiple[1]	34	33.3	1.5	0.05	11	33.4	1.1	0.03
Comfort	7	30.7	1.6	0.05	3	38.0	1.3	0.03
Nest building	3	10.7	0.3	0.03	—	—	—	—
Preening	2	428.5	3.3	0.01	2	89.0	3.0	0.03
Nest relief	1	254.0	10.0	0.04	—	—	—	—

[1] Multiple refers to more than one activity per upright time period.

days 4–21) at 1-min intervals. The time budget for 1971 was determined by analysis of the 1-min interval time-lapse films. The budget does not differ considerably from the one determined for birds incubating two natural eggs over the same period (Table 1). The total percent time spent in upright positions for the male (5.4) and female (3.6) incubating one natural and one plastic egg corresponds closely with the values obtained for birds incubating two natural eggs (male = 5.1%, females = 4.6%, Table 1). Therefore, the influence of the plastic egg on the amount of time spent in upright positions was inconsequential.

To determine the temperature loss associated with upright restless movements, I watched a pair of birds incubating one plastic and one natural egg for 54 h over a 17-day period (incubation days 23–39) in 1969. Each time the incubating bird moved, the activity and duration were inscribed on the temperature chart. Tables 3 and 4 show summaries of the events observed, their duration, and respondent temperature loss. The plastic egg occupied the back position in the nest less than half the time for the period before hatching and never occupied the front position after hatching. Temperature loss when the egg was in the front position was greater for most activities (Tables 3 and 4). This seems logical as the back egg is less exposed than is the front egg. Upright sequences of multiple activities were of longer duration than single events, such as alertness at the approach of an intruder, rotations, and comfort movements. The two nest relief ceremonies exposed the eggs for the most time of any event recorded. The egg temperature dropped 10.0° and 15.0°C on these two occasions (Tables 3 and 4).

TABLE 4

UPRIGHT RESTLESS MOVEMENTS OF MALE ADÉLIE PENGUIN IN RELATION TO TEMPERATURE OF PLASTIC EGG

	Egg in front				Egg in back			
Activity	n	Mean duration (s)	Mean temp. loss (°C)	°C/s	n	Mean duration (s)	Mean temp. loss (°C)	°C/s
Rotation	4	22.0	2.6	0.12	4	32.0	1.5	0.05
Multiple	7	33.0	2.4	0.07	3	49.3	0.7	0.01
Nest relief	1	288.0	15.0	0.05	—	—	—	—
Rotation[1]	-	—	—	—	11	20.5	0.7	0.04
Multiple[1]	-	—	—	—	9	151.1	2.3	0.02
Feeding[1]	-	—	—	—	3	249.3	2.2	0.01

[1] After hatching.

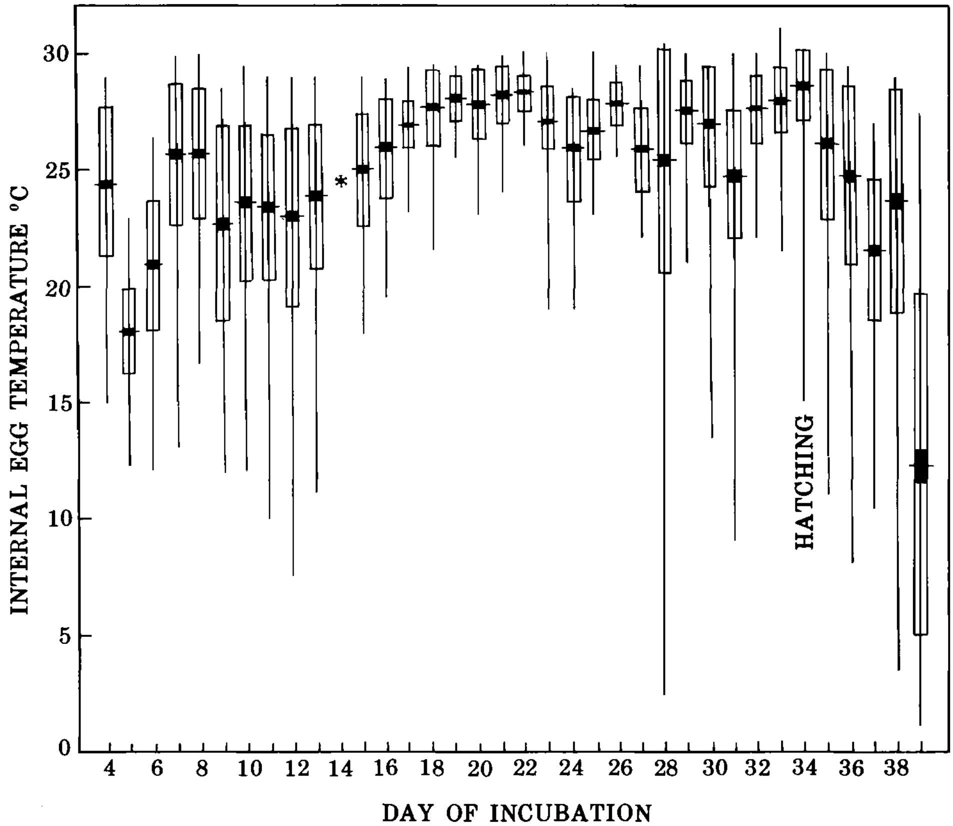

Fig. 6. Mean daily plastic egg temperatures recorded at one Adélie Penguin nest. Asterisk indicates malfunction of recording apparatus. Vertical lines indicate range, open rectangles the interval two standard deviations from the mean, solid rectangles the interval two standard errors from the mean, and horizontal lines the mean.

Figure 6 shows mean daily egg temperatures recorded at one nest for 35 days in 1971. Mean daily temperatures of the plastic egg ranged from 12.3° (day 39) to 28.6°C (day 34). These temperatures are considerably lower than temperatures recorded for a natural egg in 1969. An average temperature of 35.2°C (range 30 to 38°C) was recorded for a natural egg (in a two-egg clutch) for a 27-h period during incubation days 27 and 28.

Mean daily plastic egg temperatures showed considerable fluctuation from incubation day 4 to 9 (Fig. 6). From incubation day 15 through 22 mean daily egg temperatures gradually increased. The range of egg temperatures was more narrow for this period (18–30°C) than for days 4 to 13 (7.5–30°C). From incubation day 22 to hatching, mean daily egg temperatures showed some minor fluctuations. Temperature range was highly variable from day to day and much wider (2.5–31°C) from incubation day 28 through hatching than for days 15 through 27. After hatching mean daily egg temperatures declined.

Discussion

During incubation, Adélie Penguins in this study were 100% attentive and birds maintained prone positions from 87 to 95% of the time from laying to hatching (Table

1). Maintenance activities are limited to preening, comfort movements, and resting. By comparison, many temperate and tropical birds show 60 to 80% incubation constancy (Skutch 1962) and have additional maintenance activities such as bathing, foraging, and locomotion (see Nice 1937, Skutch 1962, Verbeek 1972). There are several probable explanations for the rigid time budget and complete constancy during the incubation period of the Adélie: (1) to maintain a temperature conducive to the most rapid development of the embryo, (2) to reduce the impact of egg predation by the South Polar Skua, (3) to conserve energy during the long fast during incubation, and (4) to reduce egg loss from penguins moving within the colony.

Maintenance of optimal incubation temperature is the most important explanation for the high percentage of time spent in prone positions. Thermograph recordings of temperatures measured in natural and plastic (Tables 3, 4) eggs showed that brief exposure of the egg caused a rapid rate of heat loss. Eklund and Charlton (1959) determined that the average egg temperature in one Adélie nest was 33.7°C over about a 9-day period at Clark Peninsula, Wilkes Land (66°15′S, 110°31′E). My data showed an average temperature of 35.2°C for a natural egg during incubation days 27 and 28 at one nest.

Little is known of the resistance to freezing temperatures in Adélie Penguin eggs, but Kendeigh (1952) stated that embryonic development proceeds more rapidly at high than at low temperatures in most birds. Weinrich (1972) found that embryonic development of Adélie Penguins was accelerated at constant temperatures above 34°C and retarded below this temperature. The fewest abnormal embryos were found at an incubation temperature of 34°C. Matthews (1945) investigated the chilling resistance of Manx Shearwater (*Puffinus puffinus*) eggs and determined that embryos could survive unattended for up to 7 days in burrows with temperatures of about 17°C. Pefaur (1974) showed that incubating Wilson's Storm Petrels (*Oceanites oceanicus*) on South Shetland, Antarctica, successfully hatched young, even though egg-neglect periods ranged from 5.4 to 7.6 h per day. Adélie Penguin embryos must be resistant to some chilling, as eggs are unincubated but protected about 12% of the time during the laying period (Table 1). However the lower temperatures at Cape Hallett would quickly freeze penguin eggs left exposed for periods as long as those in the Wilson's Storm Petrel. The exact thermal and humidity requirements and tolerances for successful hatching are still unknown, but this study demonstrated that the developing embryo experienced temperature fluctuation by day and by stage of incubation (Fig. 6).

Incubating Adélies maintained prone positions when skuas flew far overhead or alighted at the perimeter of a penguin colony. Complete constancy coupled with minimal restlessness helps protect the eggs from predation.

The adult male may lose up to 40% of its body weight from the time it arrives at the breeding grounds until relieved during incubation by the female (Sladen 1958). When relieved the male may have to traverse a considerable distance over ice to reach open water for food. These activities together represent a tremendous drain on stored fat reserves. Minimum activity during the incubation period would seem essential following periods of high activity such as territory establishment, nest building, and mating. Adélie Penguins do not neglect the clutch to forage as do some burrow-nesting Procellariiformes in the Antarctic (Roberts 1940, Tickell 1962). Genetic selection would favor those incubating penguins that reduced activity, enabling them to survive the fasting period.

Adélies nest in dense colonies ranging in size from several to over one hundred pairs at Cape Hallett (Reid 1964). Incubating birds defend the nest site vigorously. Nonincubating birds spend considerable time collecting stones from undefended areas, as well as from nests of adjacent birds. Eggs must be guarded continuously to prevent displacement by the activities of birds collecting stones.

Stonehouse (1970) suggested that some penguins may have evolved a shorter incubation period in response to the harsh antarctic environment. The Adélie has a 33.3-day (Taylor 1962) incubation period compared to the 40- to 50-day incubation period of the Yellow-eyed Penguin of temperate New Zealand (Richdale 1941b). Skutch (1962) stated that in birds whose constancy of incubation falls below 60%, the incubation period sometimes is longer than in related species that sit more assiduously. The Adélie showed little restless activity during incubation (Table 1), which may help shorten the incubation period.

The few accounts of incubation of other species of penguins make it difficult to compare behavioral requirements for successful reproduction. The Adélie incubated prone 87% of the time during the laying period. By comparison, the Royal Penguin (*Eudyptes chrysolophus schlegeli*) stands upright over the first-laid egg and only initiates incubation after deposition of the second egg (Warham 1971). Incubation time budgets have not been worked out for penguins other than the Adélie but, the wider spread of breeding dates, the longer courtship periods, and the longer egg-laying and incubation periods of some species breeding at lower latitudes (Stonehouse 1970) show that incubation may be neither so rigid nor so intense as in the Adélie.

The intensity of Adélie incubation, as reflected by the frequency of upright restless movements, is not uniform throughout the incubation period (Table 1, Fig. 3). During early, middle, and late incubation less time was spent in upright restless movements than during the laying period. Many temperate and tropical nesting species show similar trends in nest attendance during incubation. Herring Gulls have a long-continued increase and then a decrease in attentive periods towards the close of incubation (Drent 1970). Drent also demonstrated that nest temperature increased as attentiveness increased. Antarctic weather necessitates a rapid buildup in incubation intensity (Fig. 3) and attentive periods (Table 2), as Skutch (1962) suggested was generally true for polar species. Fredrickson and Weller (1972) showed that Adélies become increasingly broody toward laying, and this study demonstrated that only minor changes in intensity occurred from clutch completion to hatching. Norton (1972) found a rapid transition from desultory to nearly continuous incubation during the latter part of the egg-laying stage for two species of arctic nesting sandpipers.

Less intense incubation during the laying stage may be due to the response of incubating birds to the greater number and higher activity of nonincubating birds at that time. Incubating birds often stand upright in the nest when nonincubating birds pass through the colony or try to steal stones from nests. Table 1 shows that agonistic postures were more frequent during the laying period than during early and middle incubation.

Incubating Adélie Penguins showed considerable variation in the number and time of restless movements from day to day and among individual birds. The mean of all birds showed maximum restlessness near midday. Similarly Weeden (1966) found that the number of restless movements of arctic nesting female Tree Sparrows (*Spizela arborea*) varied highly from day to day and from individual to individual, but by averaging all observations, she was able to demonstrate a general pattern of restlessness. Variation among individual incubating birds may be due to the intensity of the incubation urge, the position of the bird within a colony, or the age and experience of the bird (Tinbergen 1960, Fisher 1971).

The activity of incubating Adélies was influenced by the light cycle (Fig. 5), but no significant relationship between ambient temperature and activity was evident. Weeden (1966) found no apparent relation between restlessness and mean daily temperature for Tree Sparrows but demonstrated that restlessness was lowest during the "night" rest and highest during the hours of 1000–1400. Kendeigh (1952) demonstrated that attentiveness in incubating House Wrens (*Troglodytes aedon*) varied inversely with ambient temperature. Other studies of arctic nesting species have shown close correlation of various activities with light intensity (Karplus 1952, Armstrong 1954, Brown 1963).

Müller-Schwarze (1968) showed a daily rhythm for general activity of Adélies at Cape Hallett but found a midday minimum rather than the midday maximum demonstrated in this study. He suggested that the minimum activity at midday was in response to dissipation of body heat because of maximum temperatures reached at that time of day. Yeates (1971) recorded several external factors such as light and temperature but found no regular rhythm of various activities for Adélies at Cape Royds, Antarctica. He concluded that the more continuous light at Cape Royds prevented distinct activity rhythms. It is suggested that the 1- to 4-h observation intervals used in other antarctic studies of diurnal rhythm do not determine activity rhythms as accurately as the 1-min interval records used in this study.

It is possible that more than one factor may control Adélie incubation activity. Some evidence suggests that social facilitation may be an important external factor in disrupting Adélie incubation. Sladen (1958) commented on the infectiousness of the ecstatic display, and Penney (1968) noted that this display often occurred in spasmodic waves involving several birds at a time. I saw the bill-to-axilla display also exhibited by several birds at the same time within a colony.

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