INCUBATION SCHEDULES OF FOUR SPECIES OF CALIDRIDINE SANDPIPERS AT BARROW, ALASKA

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Reproductive success among shorebirds nesting on the open tundra at Point Barrow (71° 18′ N–156° 47′ W) depends on effective temporal organization of incubation effort. This temporal organization must confront low temperatures, unpredictable weather, and diurnal temperature cycles, all characteristic of brief arctic coastal summers. Most shorebird eggs are laid before daily minimum temperatures exceed freezing (Brown 1968; MacLean 1969) and subfreezing temperatures may occur on occasional "nights" (18:00–06:00) throughout the nesting season. Incubation under these conditions might be expected to assume one of two forms. Shorebirds might either incubate virtually 100% of the time or might show a fluctuating incubation constancy which reflects the prevailing danger of cold-exposure to unattended eggs. A study of nest attendance between clutch completion and the start of hatching should reveal whether 24-hr periodicities and noncyclic fluctuations of incubation constancy occur, and if so, whether these correspond to fluctuations in environmental factors.

The onset and termination of incubation by shorebirds at Barrow are especially crucial to the question of scheduling. Failure to incubate during the egg-laying stage might expose fresh eggs to frost damage, yet incubation of partial clutches might advance the development of first-laid eggs as much as 4 days ahead of that of last-laid eggs. Such developmental disparities are not seen at hatching, and would be intolerable for nidifugous shorebirds, among which optimum chick survival depends on a nearly simultaneous hatch of all four chicks (Norton, pers. observ.). A second scheduling problem relating to hatching arises when adverse weather occurs just as eggs are due to hatch. Hatchlings depend on surface-active arthropod prey for several days (Holmes and Pitelka 1968), which resource may be severely reduced by cold weather (MacLean and Pitelka 1971). Is there then any evidence that adult behavior can delay or advance hatching and nest departure for a few timely hours?

The calidridine sandpipers at Barrow are appropriate subjects for comparative incubation studies to answer these questions. Four species—the Dunlin, *Calidris alpina*, Baird's Sandpiper, *C. bairdii*, Pectoral Sandpiper, *C. melanotos*, and Semipalmated Sandpiper, *C. pusilla*—are relatively abundant, and together constitute the energetically dominant avifaunal group during the breeding season in the terrestrial ecosystem near Barrow (Norton 1970b). Furthermore, their breeding biology has been extensively described in a series of recent studies (Pitelka 1959; Holmes 1966a–c; MacLean 1969; Norton 1970a). All four species nest by making shallow, sparsely insulated nest depressions in the tundra surface, in which four eggs are normally laid over about a 4-day span. This group of species, however, displays two basically different incubation systems: in *C. melanotos*, only the female tends the nest, whereas both sexes of the other three species share in incubation, usually up to hatching in *bairdii*, and through hatching in *alpina* and *pusilla*.

The present study examines incubation regimes primarily among *alpina*, *bairdii*, and *melanotos* and relates incubation schedules to the influences of nesting stage, diurnal rhythms, and prevailing weather conditions.

MATERIALS AND METHODS

More than 200 nests of *Calidris* sandpipers were found in various stages of egg-laying and incubation on an 8-km² study area adjacent to the Naval Arctic Research Laboratory at Point Barrow in 1968, 1969, and 1970. During the period of nest occupancy (egg-laying through hatching), continuous telemetric temperature recordings were obtained from nests of all four species, as outlined in table 1. Two methods were used: *nest air temperatures* (cf. Drent 1967:70) were recorded using thermistors (Yellow Springs Instrument Company, Y.S.I. #402, #421) imbedded in the floors of nests, with the sensor tip emerging into the air space at the apices of the four eggs; *dummy egg temperatures* were also recorded in 1968 and 1969 from paraffin-filled eggshells, in which a Y.S.I. #427 thermistor was cemented to the inner surface of the shell, midway between the equator and the blunt pole of the egg. Each thermistor was attached by a 17-m lead to an amplifier and to a galvanometric single-pen Esterline Angus recorder. Time error of the chart paper speed was ± 5 min per 24 hr. Temperature readings suffered a ± 3° C error because ambient temperature affected the *emf* of the battery-powered amplifier despite attempts to insulate it. This slow

TABLE 1. Total days of telemetric incubation data for calidridine sandpipers at Barrow, Alaska, 1968–70.

| Species | Nesting stage | | | | | |
| | Laying | | Incubation | | Hatching | |
	days	nests	days[a]	nests	days	nests
C. alpina	8.5	4	79	21[b]	8	5
C. bairdii	6	7	29	13	4	4
C. pusilla	4	2				
C. melanotos			30	4	4	2

[a] Days: only records representing complete, uninterrupted 24-hr sequences are used in analysis of the incubation stage (partial days used from laying and hatching stages).

[b] Includes 19 uninterrupted 24-hr records from three nests containing less than the normal four-egg clutch.

baseline drift, however, did not obscure the rapid temperature changes associated with arrivals, departures, and restless movement of the adults.

As a check on accuracy of the recorder system in detecting nest absences, 16 simultaneous visual and telemetric observation sessions of 3–4 hr each were conducted from blinds near nests. In addition, nest air temperatures and dummy egg temperatures were recorded simultaneously in three nests in order to compare information received from the two types of measurement. These observations revealed that nest absences were equally reliably detected by both systems. Nest air-temperature sensors were more sensitive to slight motions of the incubating adult, which produced sharp, temporary rises in temperature, probably as a result of momentary contact between eggs and thermistor. There was a fixed 0.5-min underestimation of length of parental nest absences because both nest air and dummy eggs rewarmed faster than they cooled, and this difference was magnified by slight friction between the recorder pen and the chartpaper. In analyzing recordings, I treated apparent absences of less than 1 min as restless movements. This treatment neither substantially overestimates restless movements (which occur normally during adults' resettling onto the nest) nor does it significantly underestimate the percentage of time adults spent off the nest (92.4% of all absences for all species were longer than 2 min).

Visits to the nests for recorder maintenance were limited, as much as possible, to 48-hr intervals in order to accumulate records of undisturbed incubation behavior throughout daily cycles. During egg-laying and hatching, however, observer surveillance increased up to several visits per day. During maintenance visits, temperature readings were made with a telethermometer (Y.S.I. 42SL, accurate to ± 0.5° C) in order to recalibrate the recorder system and to determine nest temperatures under the incubating adult. Activities of the adults occasionally changed the positions of thermistors in the nest enough to produce meaningless readings. After making a telethermometer reading, the incubating adult was flushed, and necessary adjustments of thermistor positions made.

The incubation schedules of species in which both sexes tend the nest are more complex than those of single-sex incubation. Since no continuous determination of sex of the incubating partner was attempted on alpina, bairdii, or pusilla, it is inappropriate to discuss attentiveness vs. inattentiveness, these being characteristics of individual birds rather than measures of incubation of eggs (cf. Drent 1967:15). Two interconvertible and complementary terms are required for

discussion of the simple analysis of my incubation records, and I have developed the following usage:

Attendance is the proportion of time (%) a nest is incubated by either sex.

Absence (= "break" of Drent 1967) is a period when neither parent is incubating.

$$(I). \frac{\text{(Total recorded time} - \text{sum of absence duration)}}{\text{Total recorded time}} \times 100 = \text{Attendance } (\%)$$

It is equally desirable, but far more tedious, to analyze records of these species by using sitting-spell durations of individual adults. I do not discuss sitting spells, however, because it is possible that many nest reliefs occurred too rapidly to appear as absences on the temperature records. The result would be erroneous overestimates of sitting-spell durations.

Since only the female *melanotos* incubates, incubation rhythms of this species pose no such difficulty. I continue to use the term "absence" and shall discuss sitting spells in this species:

$$(II). \frac{\text{Sum of sitting-spell duration}}{\text{Total recorded time}} \times 100 = \text{Attentiveness } (\%)$$

RESULTS

The four species of calidridine sandpipers studied were highly effective in the maintenance of a nest environment conducive to embryonic development. Fewer than 5% of all nests had eggs which failed to hatch as a probable result of chilling during inadequate incubation. Inadequate incubation can occur, however, as on an intensive study plot in 1970, where continual human disturbance coincided with a hatching failure of 30% (6 of 20 nests hatched only 2 or 3 of the 4 eggs).

INCUBATION DURING EGG-LAYING

The nest-occupancy periods of all species were distinctly divisible into three stages: laying, incubation, and hatching. Information is available on the development of incubation patterns during egg-laying for all Barrow *Calidris* species except *melanotos* (table 1). Examples of the progressively increasing nest attendance are presented for *alpina*, *bairdii*, and *pusilla* in figure 1. Nest air temperatures sampled among eggs of incomplete clutches ranged from – 1.5°C with no adults on the nest to a maximum of 18.0°C under an attentive adult (fig. 2).

The amount of incubation during egg-laying varied among species and among individual pairs. Nests of *alpina* were generally the least continuously attended of the three species investigated during egg-laying. There was no general increase in nest attendance at night when temperatures were often below freezing, although some pairs of the three species in-
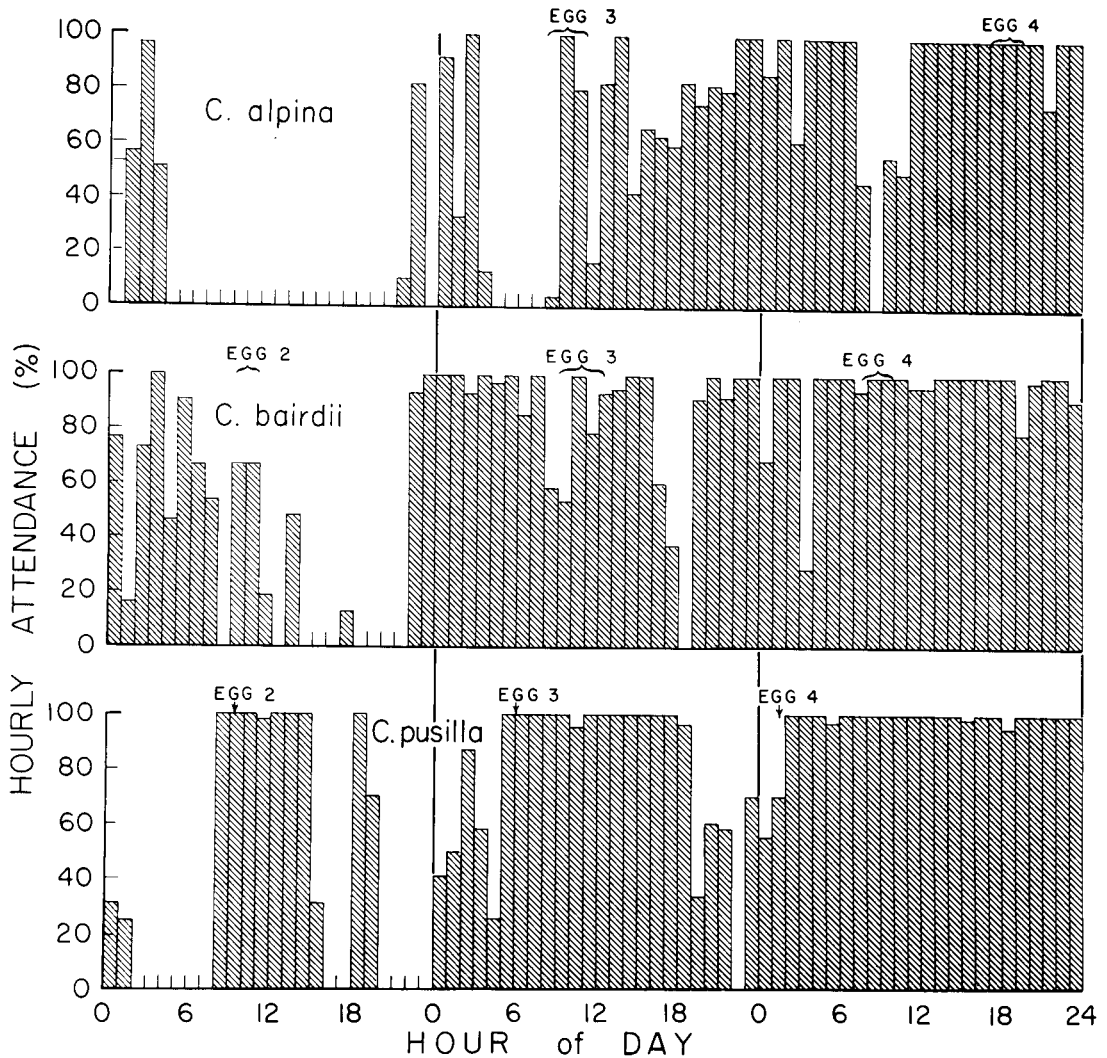
FIGURE 1. Examples of the buildup of incubation schedules among Barrow sandpipers. Attendance by hourly intervals during 3 days of egg-laying stage in individual nests of *C. alpina, C. bairdii,* and *C. pusilla.* Notations above histograms denote range of time in which direct observations indicate that an egg was laid.

vestigated did tend to incubate more during colder hours of the day.

Weather disturbances seemed to induce greater nest attendance in some cases, but not in others. In 1969, two incomplete *pusilla* nests and one incomplete *bairdii* nest were being monitored simultaneously when an unusually heavy rainshower occurred. All three nests were incubated for the duration of the storm (about 90 min). By contrast, a two-egg *alpina* clutch in 1970 remained unincubated for 16 hr, during which time driving snow completely filled the nest cup and covered the eggs. The adults returned, completed the clutch, and all four eggs later hatched. [Resistance to chilling damage appears to be maximum during the laying period before incubation begins (Norton, pers. observ.). Hatchability in the face of

exposure also declines with advancing incubation in other species—cf. MacMullan and Eberhardt 1953.]

INCUBATION AFTER CLUTCH COMPLETION

Incubation schedules usually were stabilized within hours following laying of the fourth egg, and remained relatively invariant until 1 or 2 days before hatching. Minor trends such as reduction of restless movements, shortening of mean absence duration, and progressively shorter sitting spells (*melanotos*) are evident from inspection of figures 3 and 4.

Using each uninterrupted 24-hr record as a sample unit, overall nest attendance (mean ± SE) after egg-laying among normal four-egg nests of *alpina* was found to be 97.55 ± 0.25%; among *bairdii*, attendance was 96.50 ± 0.47%.
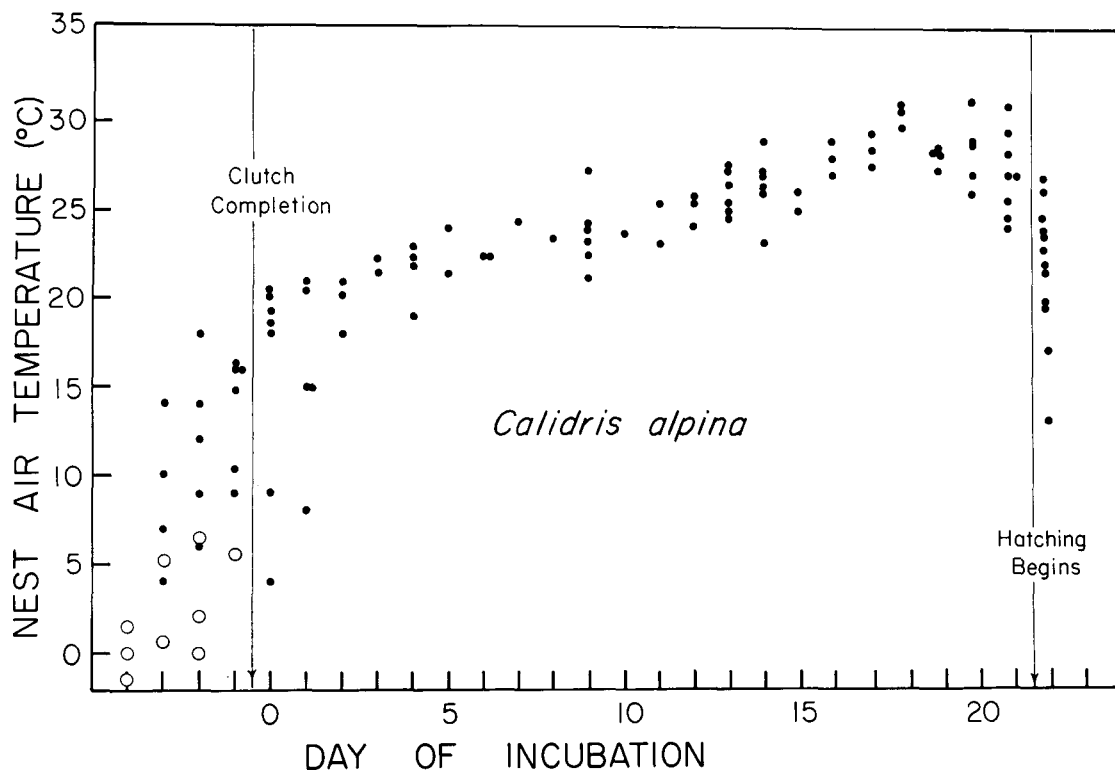
FIGURE 2.   Nest air temperatures under incubating *C. alpina* from egg-laying stage to nest departure (●), and nest air temperatures in unincubated nests during egg-laying stage (○).

Attentiveness among female *melanotos* was 84.99 ± 0.54%. Attendance of *pusilla* was not measured, but it is probably close to the values determined for *alpina* and *bairdii*.

The rather abrupt changes in *alpina* incubation schedules once the fourth egg was laid (figs. 1–3) suggest that the configuration of the clutch is an important determinant of incubation behavior in that species. Incubation records from three imperfect *alpina* nests (2- and 3-egg clutches) indicate erratic and desultory incubation schedules. Overall nest attendance during 19 recorded days from these nests was 88.73 ± 2.40%. Long absences occurred frequently, with no apparent relation to daily cycles, and hatching success was lower than normal (2 of 3, 1 of 2, and 3 of 3 eggs hatched from these nests).

Incubation schedules among the four calidridine species at Barrow show different degrees of diurnal rhythmicity. Nest attendance declined during the middle of the day in both *alpina* and *bairdii*, as a consequence of more frequent and longer absences (fig. 5). Attentiveness of female *melanotos* similarly declined because of more frequent interruptions of incubation (fig. 6). Comparison of incubation records from different nests reveals that each *alpina* and *bairdii* pair and each *melanotos*

female had a distinct individual daily schedule. If the records from all four *melanotos* nests had been combined in figure 6, the apparent diurnal rhythm of the most extensively studied bird would have been largely masked by noncorrespondence of these individual variations in schedule.

A maximum of restless movements, shown for *alpina* and *bairdii* in figure 5, precedes the daily decrease in attendance by 1–2 hr, and a minimum of restlessness occurs in mid-afternoon for each species. The regular decrease in attendance or attentiveness during warmer hours of the day suggests a possible relationship between ambient temperature and incubation constancy. Because of variability arising from other intervening influences on incubation behavior, there is no statistically significant linear relationship between nest attendance and daily mean ambient temperature. Nevertheless, the following tendencies are apparent in these data: nest attendance in *alpina* and *bairdii* increased at low ambient temperatures, with a concomitant decrease in mean absence duration. By contrast, attentiveness of female *melanotos* decreased slightly on colder days, with an increase in mean absence duration. During the few exceptionally warm days at Barrow (15°C or warmer), nest at-
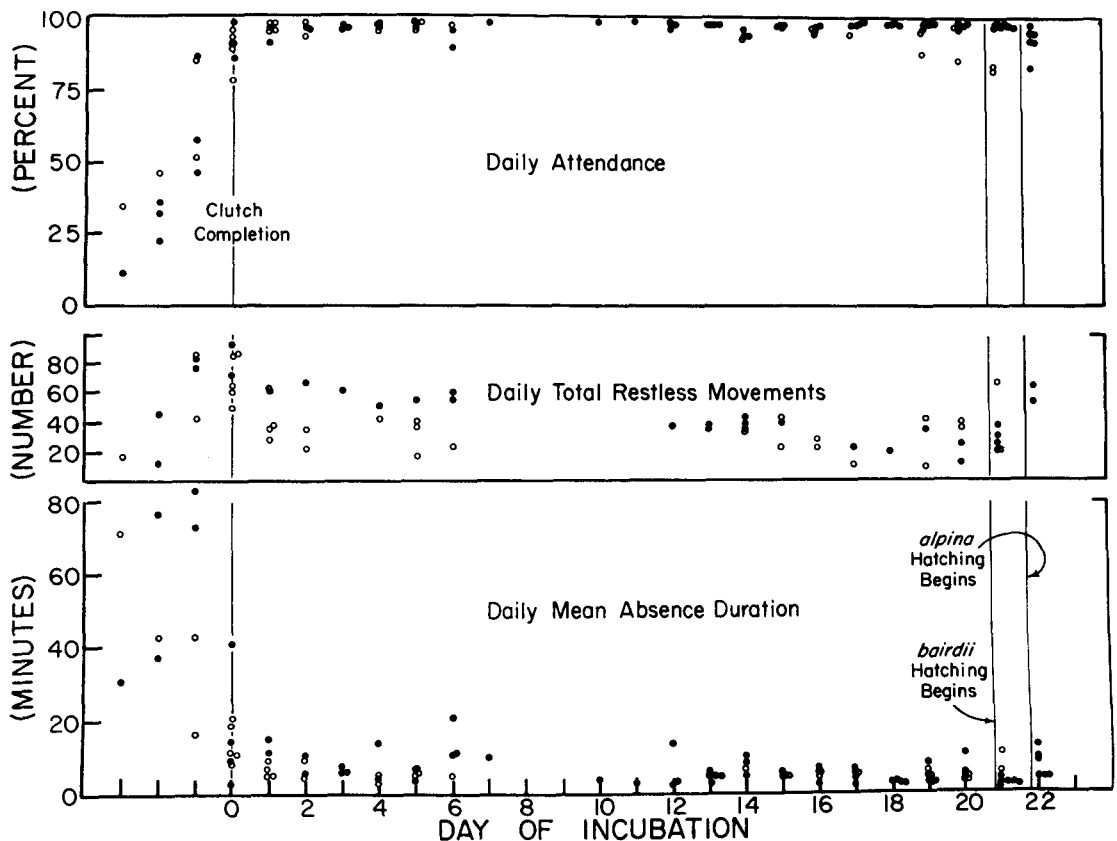
FIGURE 3. Incubation parameters of *C. alpina* and *C. bairdii* from egg-laying stage to nest departure. *C. alpina* (●), 60 recorded days from 18 nests; *C. bairdii* (○), 29 recorded days from 13 nests.

tendance in all three species was high, as absences were short and infrequent. To demonstrate the relationship between incubation schedules and environmental temperature, I separated the 1968 *alpina* incubation records into two nearly equal series, one representing "cold" days when the minimum temperature was below freezing and the maximum below +5°C, and "warm" days when the minimum temperature exceeded freezing and the maximum exceeded +5°C (table 2). This analysis

TABLE 2. Comparison of nest attendance by *C. alpina* on "warm" and "cold" days at Barrow, Alaska, 1968.

	"Warm" days (21) (min > 0°C, max > 5°C)	"Cold" days (23) (min < 0°C, max < 5°C)
Total min recorded	28,980	31,740
Min absent	720	412
No. of absences	123	100
Mean duration of absences (min ± SE)	5.88 ± 0.48*	4.12 ± 0.35*
Attendance	97.5%	98.7%

* Significance of difference between means: $P < 0.01$.

does not prove, however, that low temperatures alone inhibit nest absences, because snow, rain, fog, and high winds frequently accompanied low temperatures, and these factors may affect *alpina* behavior more profoundly than did temperature.

HATCHING

The appearance of holes in eggshells preceded hatching by 12–48 hr and coincided with changes in incubation behavior of adult sandpipers. The adults became more vocal and excitable by human observers during the last 2 days before hatching. Incubation records show a slight decrease in attendance (figs. 3 and 4), nest air temperatures became more variable (fig. 2), and there was an increase in restless movements.

Many temperature records became unintelligible once hatching had begun because of contact between damp chicks and the thermistor, but these records suggest frequent, short adult nest absences, particularly after the first egg had hatched. Visual observations confirmed the assumption that on-off rhythms in
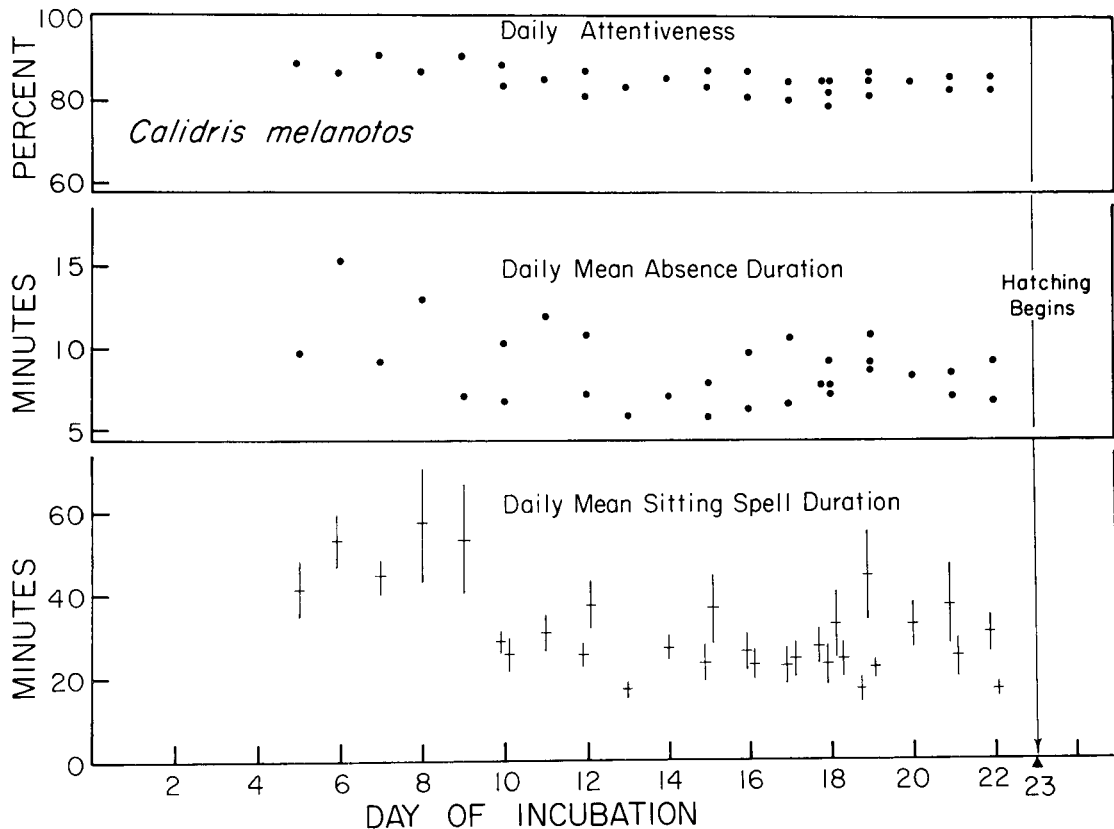
FIGURE 4.   Incubation parameters of *C. melanotos* related to nesting stage. Daily means ± SE of mean of sitting spells for all daily sitting spells except the longest (= "night rest") are shown. Data from 30 days of recorded incubation on four nests.

nest attendance quicken and lose their diurnal periodicity. Some of these absences represent eggshell removal flights by the attentive adult, while other absences were observed to be cases of the adult rising and walking a short distance, standing briefly, and then returning to resettle on the partially hatched brood.

The most complete observations of processes leading to hatching were made on *alpina*, and these suggest that variations in adult behavior and in synchrony of hatching are related to prevailing weather conditions. During mild weather, all four eggs often hatched within several hours between midnight and noon, and the hatchlings left the nest by early or mid-afternoon. During cold and foggy, rainy, snowy, or windy weather, hatching synchrony was less apparent, as the interval between the first hatch and nest departure increased. Hatching commonly commenced in late afternoon of a cold day, and was not complete until the following morning. Nests hatching during cold weather seem to have required about one more day of incubation (interval between clutch completion and nest departure) in *alpina*, where this period at Barrow was found

to vary between 21.5 and 23 days, and likewise among *bairdii*, whose incubation period varied between 19.5 and 21 days. (The incubation period of *melanotos* at Barrow remains unknown, as predation claimed the only nest of that species discovered during egg-laying; it is assumed to average 23 days in this study.)

Just prior to and during natural hatching, incubation was more constant and nest air temperatures higher during adverse weather than during mild weather. Two contrasting examples of the final 2.5 days of *alpina* incubation are presented in figure 7. The upper nest record represents a delayed hatching during rainy and snowy weather (temperature range: −1 to +4°C) in which adult attendance remained high even after the first egg hatched, then declined abruptly at nest departure. The lower record represents a synchronous hatching during sunny, calm weather (temperature range: +5 to +10°C). There was a rather steady decline in adult nest attendance, beginning a few hours before any eggs had hatched and continuing until nest departure, about 12 hr after the first egg hatched. Similar but less extensive observations were made
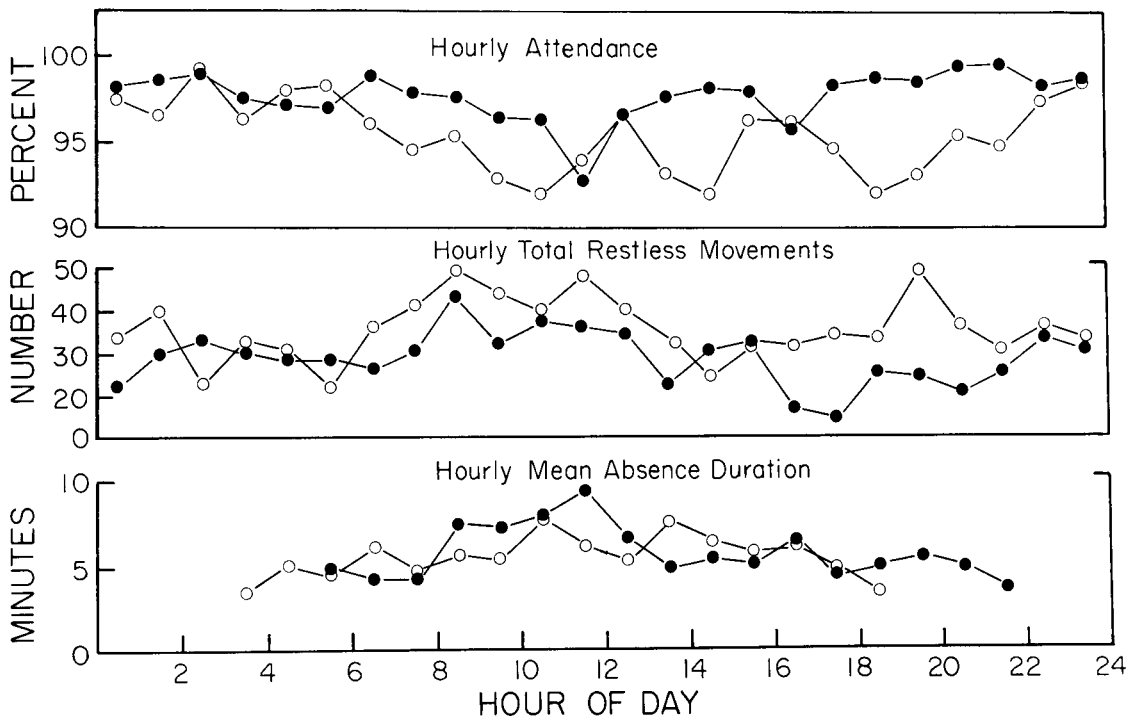
FIGURE 5. Diurnal periodicity of incubation parameters in *C. alpina* and *C. bairdii*. Hourly mean absence duration shown only for those intervals when more than a total of five absences occurred. *C. alpina* (●), 60 recorded days from 18 nests; *C. bairdii* (○), 29 recorded days from 13 nests.

on *bairdii* and *melanotos* hatching. Part of the decline in *bairdii* attendance at hatching may arise from the departure of some adult females from Barrow once their nests began to hatch (MacLean 1969).

NOTES ON OTHER INFLUENCES ON INCUBATION SCHEDULES

Physiological condition, genetic constitution, experience of adults, social factors, and predation probably are all related to nesting efforts and incubation constancy of sandpipers. The following anecdotal observations support these assertions.

A female *alpina*, which suffered a leg injury during egg-laying in 1970, laid only two eggs, the second of which entirely lacked pigmentation. Both eggs hatched after a prolonged incubation period (more than 22.5 days).

At another *alpina* nest, in 1968, the male deserted after being injured in a small mammal snap trap. For 3 days following the male's desertion, temperature records indicate that the banded female daily left the nest in late morning for 6–10 hr. On the fourth day, the incubation rhythm returned to normal, at the same time that two unbanded *alpina* began to be seen regularly in the vicinity of the nest, although I could never determine that either

of the strange birds actually participated in incubation.

Clutches of less than four eggs are rare, except as replacement clutches laid by *alpina* following destruction of the first nest. A female *alpina* banded in 1968 on a three-egg clutch returned in 1970, and again laid a nonreplacement three-egg clutch.

Returns of banded birds further indicate that first-year *alpina*, a small proportion of which return to Barrow, begin nesting significantly later than do older birds (Norton, pers. observ.; Pitelka, pers. comm.).

The polygynous mating system of *melanotos* has a ramification with unknown consequences for the constancy of incubation. During the early stages of incubation, while male *melanotos* are still present on the tundra, any female leaving the nest to forage is often pursued and detained in copulation by at least one male. Whether this risk acts to increase or decrease nest attentiveness is unclear, but the vigilance of males appears to reinforce the furtiveness of movements by females temporarily off the nest.

Incubation behavior has been shaped to an unknown extent by vulnerability of the nest to predation. *Calidris* species suffer varying degrees of nest predation by jaegers and gulls
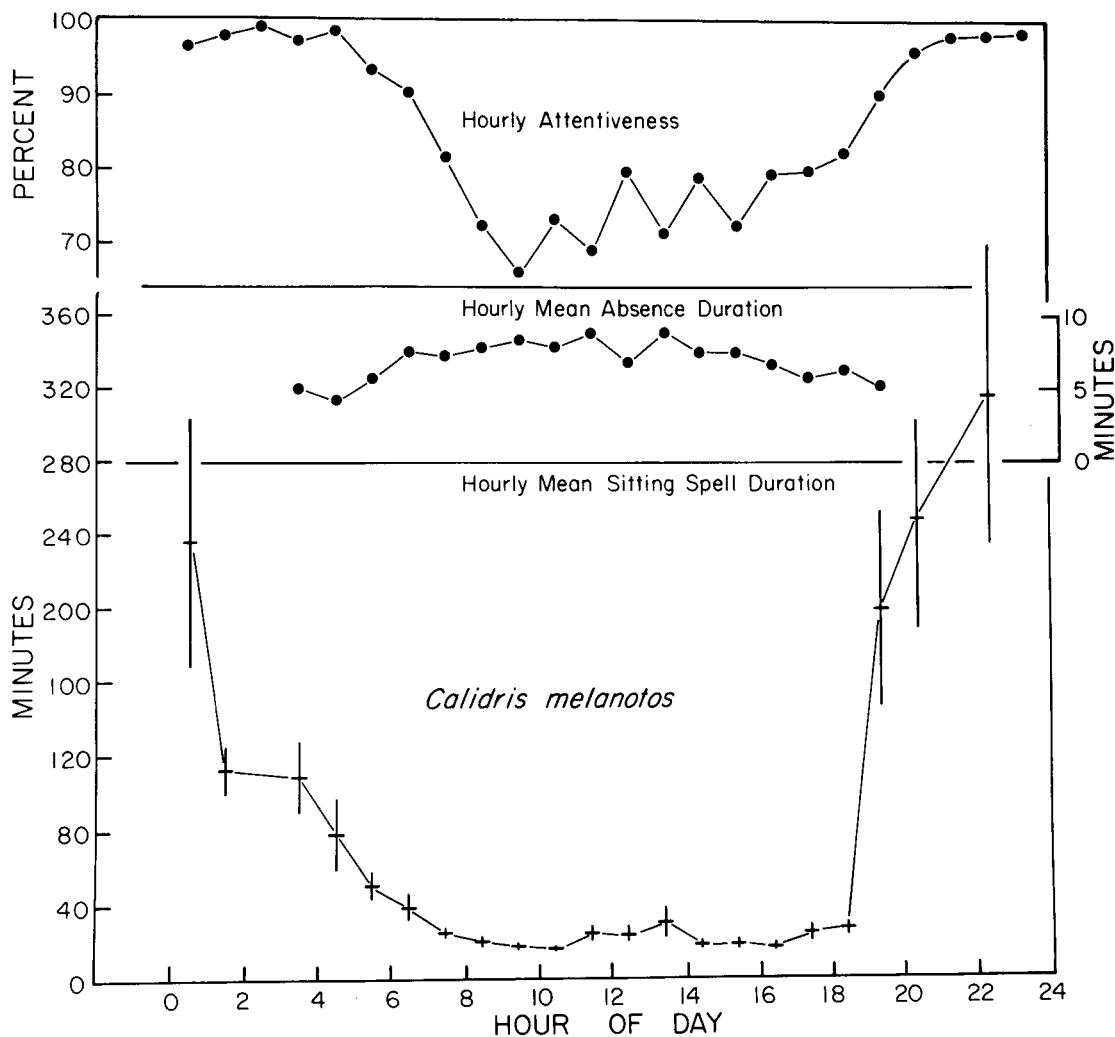
FIGURE 6. Diurnal periodicity of incubation parameters in *C. melanotos*. Hourly mean absence duration shown only for those intervals when more than a total of five absences occurred; hourly mean ± SE of mean duration of sitting spells commencing per hourly interval, including the longest sitting spell ("night rests"). Data from 13 recorded days at a single *melanotos* nest.

at Barrow. This avian predation is most severe among *bairdii*, whose nests are most open to view from above, and least severe among *melanotos*, whose nests are most effectively concealed by dense grasses and sedges surrounding and overhanging the nest. Of 102 *bairdii* nests in this study, 58 were lost to predation (some to weasels rather than avian predators), while only one of 15 *melanotos* nests was lost, despite the greater proportion of time *melanotos* nests are left uncovered. Incubation constancy is probably an important deterrent to jaeger predation among *bairdii*, and possibly *pusilla* (Safriel, pers. comm.). Incubating adults of these two species are more reluctant to leave the nest, and generally flush at shorter distances than do either *alpina* or *melanotos*.

DISCUSSION

INCUBATION STAGE

A fairly high level of nest attendance between clutch completion and hatching appears to be a necessary, but not a unique, attribute of arctic *Calidris* sandpipers. Many nonarctic breeding birds have similar high levels of nest attendance, as, for example, 90–98% in various species of gulls (Drent 1967). The female Capercaillie, *Tetrao urogallus*, incubates 95.1% of the time in Swedish Lapland (Lennerstedt 1966), thus surpassing *C. melanotos* in attentiveness. Skutch (1962) estimated nest attentiveness among a variety of Central American birds and found that many species of single-sex incubators also surpass the 85% attentiveness of female *melanotos*.
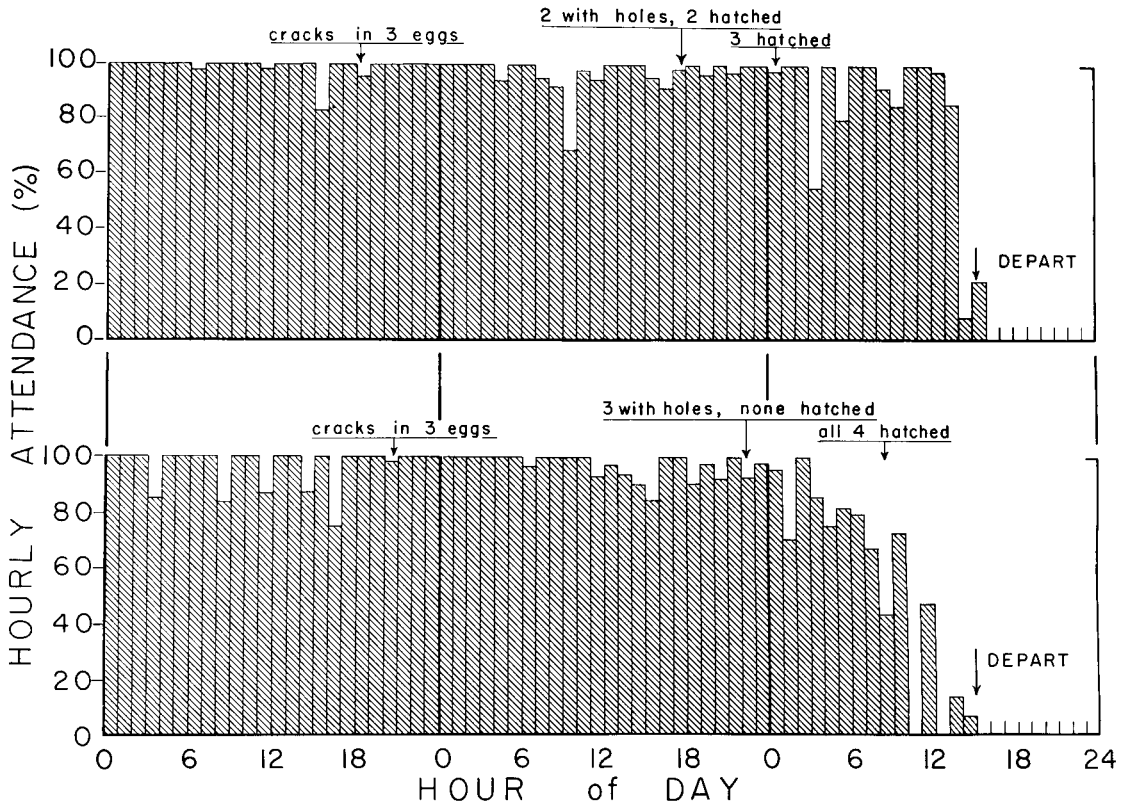
FIGURE 7.   Contrasting examples of the termination of incubation in two nests of *C. alpina*. Hourly attendance during last 2.5 days of nest occupancy. Above: 2–4 July 1968, during snowy weather. Below: 22–24 July 1968, during sunny and calm weather. Notations above histograms denote direct observations made on hatching progress in a given hourly interval.

The data on incubation of imperfect *alpina* clutches further indicate a margin of safety between the 97.5% attendance of normal four-egg clutches, and the 89% attendance of two- and three-egg clutches, at which level, embryonic chilling injury probably begins to be a regular consequence in that species. The configuration of the normal four-egg shorebird clutches is ideal for heat conservation (Norton 1970a), a fact which probably allows for normally observed nest absences to occur without rapid embryonic chilling. Furthermore, the embryos of *Calidris* species show a certain degree of resistance to chilling damage which could be significant in the event of unusually long parental absences (Norton 1970a and *Arctic*, in press).

The effectiveness of incubation, resulting in rapid embryonic development and negligible mortality despite uncertain climatic conditions at Barrow, appears to depend most closely on differential incubation responses by the adults to changing environmental conditions. The diurnal periodicity of nest absences among two-sex incubators (*alpina* and *bairdii*), al-

though not pronounced, nevertheless results in more constant nest coverage during the coldest part of the 24-hr day. Likewise, *melanotos* females, whose diurnal rhythmicity is more pronounced, are most attentive at night.

Day-to-day changes in incubation constancy reflect variations in weather conditions (table 2) especially just before and during the critical period of hatching (fig. 7).

There are a number of possible mechanisms which would relate the observed daily (cyclic) and day-to-day (noncyclic) responses of incubation performance to climatic variation. The most plausible to consider are the following: endogenous circadian activity rhythms and their exogenous controls (*Zeitgeber*), the relationship between foraging rhythms and incubation schedules, and direct responses of the incubating adults to nest microclimate.

Mechanisms accounting for diurnal rhythms of incubation constancy may be sought in a careful consideration of the similarity between *alpina* and *bairdii* schedules. Adults of both species showed a peak in restless movements

4–5 hr before local noon (13:25 Alaska Daylight Time) and a maximum frequency and duration of nest absences 2–3 hr before local noon (fig. 5). This similarity suggests that each species responds to the same local cues in the setting of activity rhythms. The impression that local *Zeitgeber* are important is strengthened when we consider that these two species must adjust their activity rhythms in opposite directions annually. *C. alpina*, in migrating eastward from Asiatic wintering grounds centering on about 135°E (MacLean and Holmes 1971; Norton 1971), must advance its activity cycle by about 5 hr. By contrast, *C. bairdii* must retard its activity cycle by about 6 hr in migrating northwestward from wintering areas centering on about 65°W in South America. These patterns recall the more rapid experimental translocations of honeybees (Renner 1960). The modest diurnal fluctuation in incubation constancy in these two-sex incubators might be explained in terms of greater nest attentiveness of one sex if, for example, females predominantly incubated at night and males by day, as suggested by Heldt (1966) and Soikkeli (1967). But preliminary results from 48-hr periods of observation at 2-hr intervals at a number of *alpina, bairdii*, and *pusilla* nests (Norton, pers. obs.; Safriel, pers. comm.; MacLean, pers. comm.) failed to reveal such a tendency. Adults at many nests had a rhythm of alternation which, if continued, would have placed the one sex on the nest at progressively earlier or later hours each day. Therefore, either incubating adult responds to cyclic environmental cues.

The nature of local cues which entrain the daily activity rhythms at Barrow remains uncertain. Incubating birds may respond directly to light intensity and ambient temperature. Armstrong (1954) and Cullen (1954) have cited evidence relating activity of birds to light in the far north, and Kendeigh (1952) and Haartman (1956) related incubation performance to ambient temperature. Light intensity and tundra surface air temperatures covary closely at Barrow, where Kelley and Weaver (1969) found that both parameters reach maximum values at local noon on cloudless days. This close covariance makes it impossible presently to evaluate separately the importance of light and temperatures at *Zeitgeber*.

Foraging opportunities may determine the incubation rhythm more directly than does light or temperature. Nest absences among female *melanotos* were concentrated during the lighter and warmer hours, 06:00–18:00.

During these absences, *melanotos* spent nearly the entire time feeding, according to observations of banded birds. Although the sun does not set and there is no darkness to prevent foraging at night, light intensity at midnight is only about 30% of that at noon (Dunbar 1968). Birds, being "visual animals," can be expected to capitalize on optimum visibility. Moreover, warmer temperatures may make insect prey more active, hence more easily detectable to the Barrow sandpipers.

Evidence for direct responses in incubation behavior to microclimatic conditions is difficult to obtain in a field study, where one cannot experimentally screen out other intervening variables. Von Haartman (1956), Burley (1968), Franks (1967), and Drent et al. (1970) have successfully performed manipulations of the type required for this analysis in other species. Nevertheless, sandpipers in the present study were undeniably sensitive to certain obvious conditions in their nests. The anomalous behavior at two- and three-egg nests among *alpina*, the occasional abandonment of nests when flooding occurred during peak snowmelt, and the normal deterioration of incubation schedules when eggshells cracked as a result of either partial predation or of impending hatching—these are examples of such sensitivity.

Differential incubation responses to climatic events probably depend on a combination of all three factors under discussion: endogenous daily activity rhythms; competition from foraging schedules; and direct responses to nest microclimate. Predicting how these influences act in concert to shape incubation schedules is greatly simplified by invoking the concept of "comfort mechanisms." Drent (1967:105) has argued well for the point of view that appropriate incubation responses to climatic events represent primarily comfort mechanisms for the adult birds, which only secondarily result in protecting the nest from environmental extremes. This concept, stated slightly differently, views adult responses as proximately triggered by environmental conditions, but ultimately shaped and refined by the differential survival of broods from protected nests. In this scheme, the cyclic variations in incubation behavior result from adults' sitting down out of the wind during the coldest hours of the day and concentrating the foraging effort during the warmer and probably more productive hours. Noncyclic incubation responses are derived from the same comfort-enhancing responses, as well as from comfort factors arising from the configuration of the clutch,

in which any imperfection reduces the tendency to incubate (cf. Baerends et al. 1970).

A certain degree of variability in incubation responses to environmental conditions is tolerable because of the heat-conserving configuration of shorebird nests and the resistance of embryos to frost damage (Norton, in prep.). The incubation stage of the species studied here therefore represents essentially a uniform "plateau" of behavior. There were no obvious trends in schedules between clutch completion and hatching (figs. 3 and 4) which could not be ascribed to variations in individual incubation responses or to the generally improving weather over the course of incubation. Despite these individual variations and occasional long nest absences in each species, egg mortality from inadequate incubation is virtually unknown except in the cases of two- and three-egg clutches, complete nest abandonment, and extreme human disruption of incubation schedules.

The contrasting social systems of monogamous *alpina, bairdii,* and *pusilla* on one hand, and polygynous single-sex incubating *melanotos* on the other, lead to basically different incubation strategies. Incubation by two sexes alleviates direct competition between foraging and incubation activities. Female *melanotos* must satisfy the energetic demands of incubation at the expense of incubation constancy. MacLean's (1969) data on body fat indicate that in a normal or mild season, *melanotos* are able to maintain and even increase body fat during the incubation stage, but under severe conditions, incubation may become inadequate as foraging rhythms encroach lethally on incubation time. The tendency for frequency and duration of *melanotos* nest absences to increase during adverse weather may be due both to an increased energetic expense of incubation and to greater difficulty in securing an equivalent quantity of insect prey. In the subarctic, the female Tree Sparrow, *Spizella arborea,* shows the same general reduction of incubation performance during adverse weather (Weeden 1966) as seen in *melanotos.* This relationship between foraging and incubation performance, as it depends upon weather, deserves examination in other arctic species of single-sex incubators. In particular, those species with relatively smaller, hence faster-cooling, eggs than *melanotos* would appear to require a correspondingly greater embryonic cold tolerance to survive parental nest absences devoted to foraging. Such species include the peculiar Temminck's Stint, *Calidris temminckii* (Hilden 1965; Lack

1968), the Sanderling, *Calidris alba* (Parmelee 1971), phalaropes, and passerines.

ONSET AND TERMINATION OF INCUBATION

The coaction of adult behavior during onset and termination of incubation appears to be highly important in synchronizing hatching and in setting the moment of nest departure. The incubation stage, beginning with clutch completion and ending with the beginning of hatching, was characterized above as a stable plateau of behavior with an overlying variability permitted by the margin of safety between normal and minimally adequate incubation. By contrast, hatching and nest departure are critical periods during which this margin of safety disappears. Most mortality is concentrated in the first 24 hr after hatching (Soikkeli 1967). A chick which is slightly retarded at hatching, or one weakened by early hatching and a long wait for its siblings to hatch, has little chance of survival. Broods which leave the nest in a period of low temperatures and precipitation are also at a general disadvantage.

The buildup of nest attendance during egg-laying among these birds (fig. 1) is remarkable for its quick transition from erratic to stable. This transition seemed to occur in a 24–36 hr period in each species, earliest in the egg-laying stage among *pusilla,* and latest among *alpina.* Many nesting gulls, by contrast, persisted in nightly abandonments of the nest several days after clutch completion, although some incubation took place during the laying stage (Drent 1967). Observed nest air temperatures increased with the progress of egg-laying in *alpina* (fig. 2), but were highly variable, and often only 5–10°C warmer under sitting adults than in unattended nests. I have argued elsewhere (Norton 1970a) that the desultory incubation during the laying stage, followed by rapid buildup of continuous incubation, represents a "compromise" between the danger of allowing eggs to freeze and the danger of inducing too much development in first-laid eggs. The actual developmental disparities among embryos should be determined by examination of a freshly completed clutch.

The breakdown of incubation schedules as hatching proceeds appears to be initiated by the development of irregularities in the eggshells, and possibly other cues. In the absence of such sensible cues, the adults may continue to incubate for long periods of time, as I have recorded quite normal-appearing incubation rhythms on the 33rd day after clutch completion (10–11 days overdue to hatch) in an in-

fertile *alpina* clutch. It is during this period of decreasing nest attendance that any disparities in development arising during egg-laying must be compensated for by imperfectly understood mechanisms affecting the timing of hatching. Vince (1966, 1968) demonstrated that social facilitation of hatching in quail chicks depends on auditory stimulation among chicks just prior to hatching. Such auditory cues may also be instrumental in sandpipers, because the near-term embryos tap the inside of the shell loudly enough for human perception at a distance of at least 10 cm. Mechanical and thermal cues may arise from the increased rising and settling of the adult and a resulting fluctuation of nest temperature, especially during favorable weather, may stimulate hatching. Oppenheim (1968) showed that chicken and duck embryos were responsive to light just before hatching, and light must pass through the thin eggshells of calidridine sandpipers when the nest is unattended. The simplest explanation relating variability in the observed hatching time to incubation behavior is that a fluctuating series of stimuli (auditory, mechanical, thermal, and visual) tends to accelerate hatching processes (as during warm weather), while a monotonous environment tends to delay hatching (as during adverse weather).

SUMMARY

Incubation by four species of calidridine sandpipers at Barrow, Alaska, was analyzed by telemetric nest temperature recordings and by direct observation during three field seasons. In the Pectoral Sandpiper, *Calidris melanotos*, only the female tends the nest, whereas both sexes share in incubation in the Dunlin, *C. alpina*, Baird's Sandpiper, *C. bairdii*, and the Semipalmated Sandpiper, *C. pusilla*. Both the single-sex incubation system of *melanotos* and the two-sex system of the other three species must be organized so that embryos within each clutch develop and hatch simultaneously, despite low ambient temperatures and unpredictable weather. The salient features of incubation schedules among these sandpipers were found to include:

1) A rapid transition from desultory to nearly continuous incubation during the latter part of the egg-laying stage among the two-sex incubators (*melanotos* data lacking in laying stage);

2) Nest attentiveness of 85% by female *melanotos*, nest attendance of 96.5% by *bairdii* pairs, and 97.5% by *alpina* pairs, between laying and hatching (*pusilla* data lacking from this stage);

3) A strong diurnal periodicity in incubation parameters of *melanotos*, weaker periodicity among *alpina* and *bairdii* pairs, which rhythms functionally afforded more constant covering of all nests during colder hours of the "night" (18:00–06:00) despite the continuous daylight at Barrow;

4) Only minor changes in incubation schedules for all species over the period between laying and hatching, but profound and rapid schedule modifications between laying and incubation stages, and between incubation and hatching stages;

5) A weak correlation between adverse weather conditions and incubation constancy among *alpina* and *bairdii*, which became highly pronounced (although difficult to measure) as critical hatching processes began;

6) Optimization and synchronization of hatching time by stimuli largely controlled by adult behavior just prior to and during hatching.

ACKNOWLEDGMENTS

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