THERMAL ENVIRONMENT OF THE NEST AND RELATED PARENTAL BEHAVIOR IN SNOWY PLOVERS, *CHARADRIUS ALEXANDRINUS*

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Snowy Plovers (*Charadrius alexandrinus*) usually nest in bare, unvegetated habitats (Bent 1929). One such locality is the Great Salt Plains, Alfalfa Co., Oklahoma, where daily maximum air temperatures in exposed areas are commonly above 40°C during the breeding months. The nests are simple scrapes on slight elevations and are highly exposed since the nearest vegetation (prairie grassland) is often several hundred meters away. Likewise plovers on the Great Salt Plains often locate their nests away from any large driftwood or debris, thus depriving the eggs of thermal moderation from such sources (Purdue in press). Incubation studies on other charadriiform species have been conducted in cool (Norton 1972) or mild (Drent 1970) climates and except for the work of Howell and Bartholomew (1962), Boyd (1972), and Hall (1958), little has been done with charadriiforms breeding in hot climates. My purposes are to characterize the thermal environment in which Snowy Plover eggs are maintained on the Great Salt Plains of northwestern Oklahoma and to relate this to the behavior of the parents.

METHODS

Temperatures of the nest environment were measured with a series of strategically placed thermistors. Egg temperatures were monitored by implanting a Yellow Springs Instrument (YSI) No. 402 thermistor. A hole was drilled in the side of an egg, formaldehyde was injected, and the thermistor was positioned with the sensing tip in the middle of the egg. Duco cement sealed the hole. One such egg was substituted in a nest and a second was placed on the ground nearby. For some nests a flattened thermistor (YSI No. 409) was attached to a supporting wire and positioned so that the temperature at the top of the cluster of eggs (brood patch temperature if an adult bird were incubating) was sensed. Air temperature was monitored with YSI No. 401 thermistor 5 cm above the ground a few meters from the nest. All thermistor leads were connected to a YSI Tele-thermometer in an automobile up to 100 m away. Readings were made every 10 min from 0430 to 2300 with the majority during the daylight hours. Once every 60 to 90 min surface temperature was measured around the nest with a Barnes I. R. Field Thermometer. Air movement was measured with a small, windmill-type anemometer placed on the ground.

The automobile also served as an observation blind from which adult behavior was observed with binoculars or spotting scope; thus moment-to-moment changes in parental behavior were related to temperature readings. Parental activities around the nest were noted, such as presence or absence, sitting or standing, and transference of incubation duties. Subsequently, this record was split into 5-min segments and scored. If a bird was present for more than 50% of the 5-min period, the nest was considered attended. Scores were then accumulated and related to appropriate factors (time since initiation of incubation, air temperature, and time of day). These data were treated statistically with replicated goodness of fit (G-statistics) for determining significant differences and *a posteriori* tests for finding deviant groups by simultaneous testing procedures (Sokal and Rohlf 1969). Six nests representing a total of 207 hours were so analyzed. Brood-patch temperature and incubation behavior were compared to given air temperatures by noting whether the attending bird was sitting or standing over the eggs.

RESULTS AND DISCUSSION

In a review of incubation in birds Drent (1973) reported that several species show positive correlations between internal egg temperature and air temperature while others do not. Temperatures of Snowy Plover eggs on the Great Salt Plains show a strong correlation with air temperature (fig. 1)—to the extent that to assign a "representative measurement" (Drent 1973) of egg temperature independent of air temperature for the plover would be

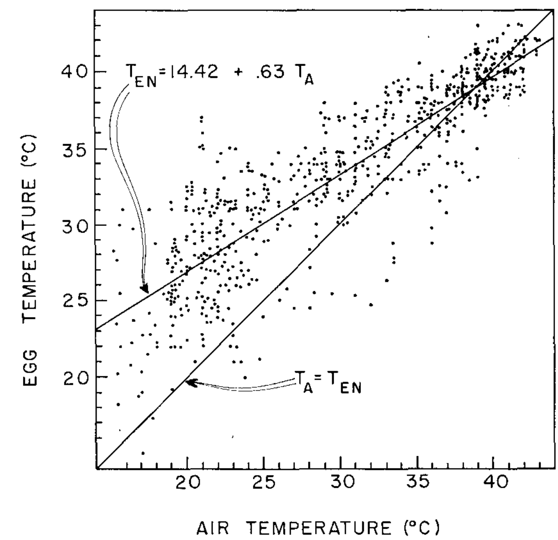

FIGURE 1. Effect of air temperature on egg temperature. T_A = air temperature and T_{EN} = temperature of egg in nest. Regression coefficient is significantly different from zero ($P < 0.001$).

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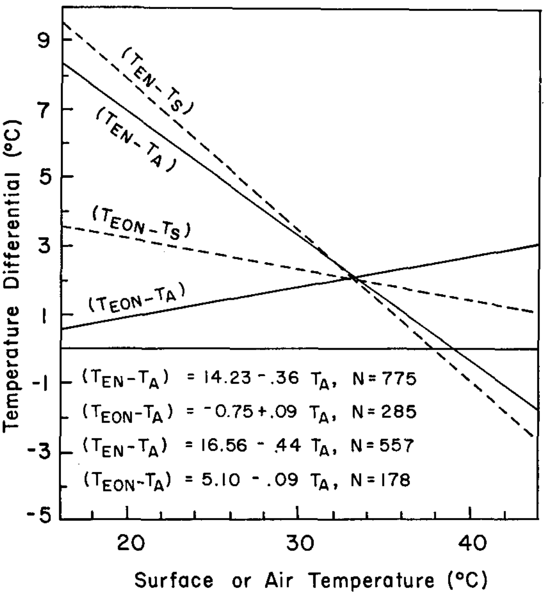

FIGURE 2. Effect of parental behavior on egg temperature. T_A = air temperature, T_S = surface temperature, T_{EN} = temperature of egg in nest, and T_{EON} = temperature of egg out of nest. All four regression coefficients are significantly different from zero ($P < 0.001$).

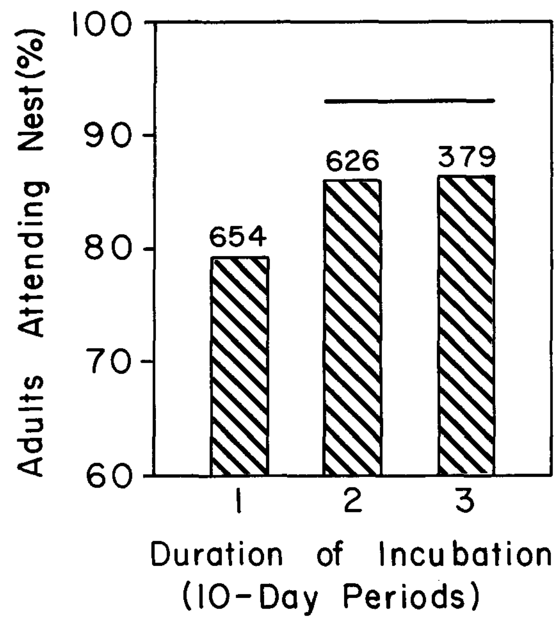

FIGURE 3. Effect of duration of incubation on adult attentive behavior. Horizontal line indicates homogeneous groups according to STP test. Sample size is indicated above each bar.

arbitrary. Two factors contribute to this observation. First, mainly diurnal observations were made, and brooding behavior was frequently interrupted by activities such as foraging, picking around the nest, and egg turning. Such activities probably do not occur as frequently at night; thus, nocturnal egg temperatures probably would be higher than air temperature and the correlation with air temperature would be reduced. Russell (1969) demonstrated this for desert-dwelling doves as did White and Kinney (1974) for weaverbirds. Second, the use of a dead egg to characterize egg temperatures does not allow for the effect of embryonic heat production.

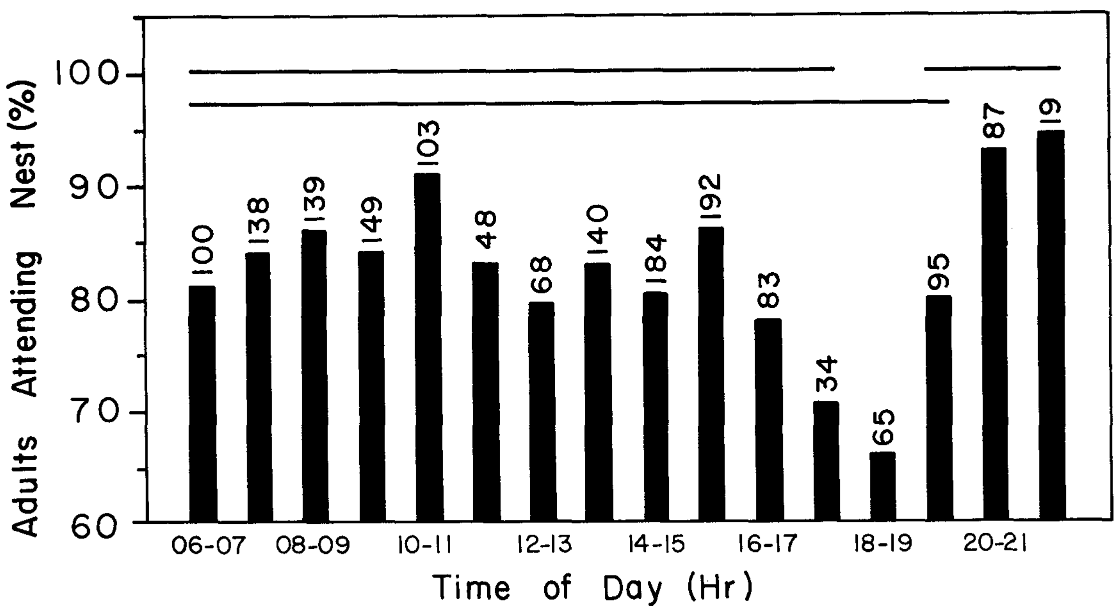

FIGURE 4. Effect of time of day on adult attentive behavior. Horizontal lines indicate homogeneous groups (STP test). Sample size is indicated above each bar.

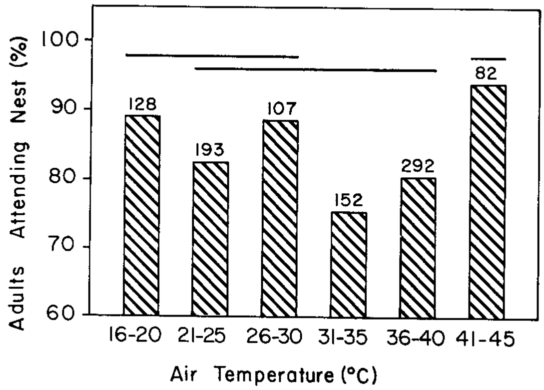

FIGURE 5. Effect of air temperature on adult attentive behavior. Horizontal lines indicate homogeneous groups (STP test). Sample size is indicated above each bar.

Drent (1970), using a respirometer on Herring Gull (*Larus argentatus*) eggs, found that after the 14th day embryonic heat production played a significant role in elevating egg temperature above that of the air immediately in contact with the egg.

My data from dead eggs show that lethal conditions occur on the salt flats and that parental incubation behavior moderates fluctuation in egg temperature. The maximum egg temperature recorded for eggs outside the nest was 48°C as compared with 43°C for eggs in the nests. The latter temperature lasted only briefly toward the end of a period when the parents had not attended the nest. Eggs outside the nest more closely parallel ambient temperatures than do eggs in the nest (fig. 2). Eggs in the nest became cooler than unattended eggs when the air temperature rose to about 33°C. Also, eggs in the nest are cooler than ambient conditions at air and surface temperatures of 38–39°C; this does not occur in unattended eggs. Thus, there was a striking contrast between the temperatures of unprotected eggs, which roughly paralleled ambient conditions, and of the protected eggs which were less affected by the weather.

Several adult behaviors affect egg temperatures. As with other species (Drent 1970), time devoted to the eggs increased with duration of incubation (fig. 3). Time of day was also correlated with incubating attentiveness (fig. 4). Plovers were quite attentive most of the day, but became distinctly less attentive in late afternoon. This coincided with a major foraging period just before nightfall. No comparable decrease occurred in the early morning hours which represented a second major foraging period. Kendeigh (1952) found a drop in attentiveness during the daylight hours for House Wrens (*Troglodytes aedon*), but it was not as sharp as that shown in figure 4. Norton (1972), working with Arctic-breeding

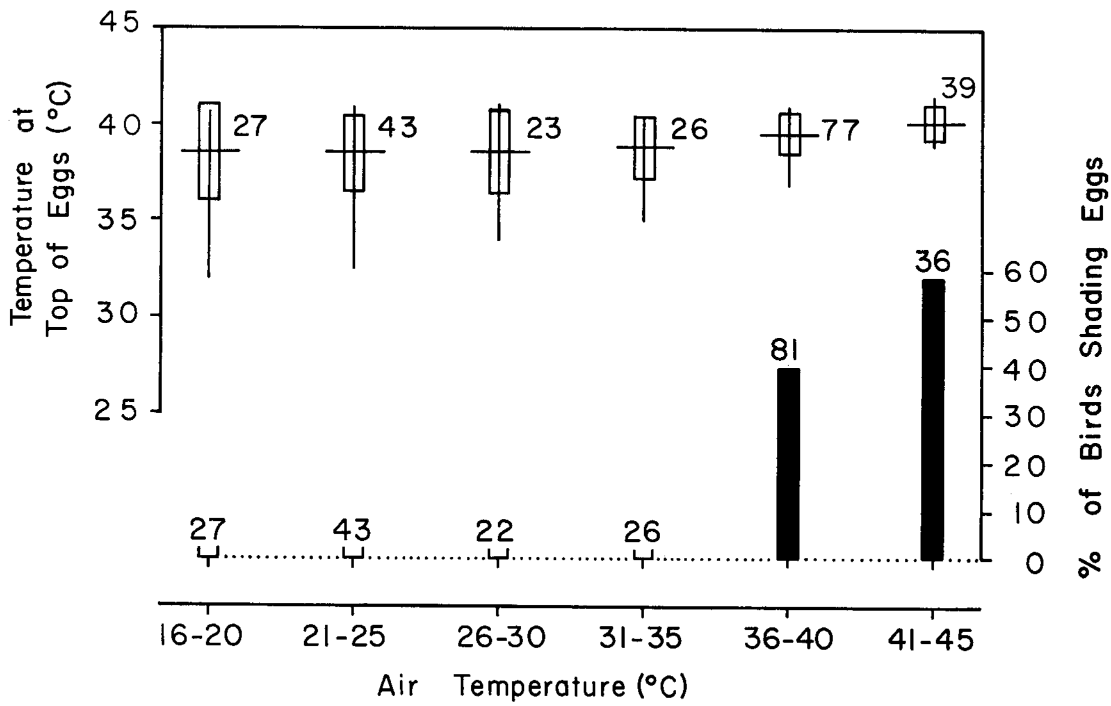

FIGURE 6. Effect of air temperature on standing behavior and temperature on top of eggs. Sample size is indicated for each category.

sandpipers, also found decreased attention during the day.

Attentiveness was significantly reduced when the ambient temperature was between 31° and 40°C (fig. 5), a thermally moderate range for most birds and comparable to the zone of stable regulation that White and Kinney (1974) found for weaverbirds. At these temperatures the adults can be away from the nest with little thermal danger to the eggs. Attentiveness was maximal at temperatures of 41–45°C, which probably were near lethal conditions. This agrees with von Haartman's (1956) observations on several other species of birds. Similarly, Howell and Bartholomew (1962) found that when a Sooty Tern (*Sterna fuscata*) nest is exposed to intense midday heat, the adults are extremely tenacious in staying with their eggs.

Moderate air temperatures often occur late in the afternoon, when nest attentiveness drops. Also, the first third of the incubation period tends to be early in the season, increasing the likelihood of moderate thermal conditions. Thus, the factors correlated with nest attentiveness in the Snowy Plover are interrelated.

At high temperatures, the adults of many species of birds stand over the nest so that a shadow falls on the eggs; Boyd (1972) and Rittinghaus (1961) have reported this for the Snowy Plover. Figure 6 clearly indicates that the frequency of standing is a function of ambient temperature. At air temperatures above 41°C standing occurs more frequently than sitting, and there is no significant increase in the temperature at the top of the eggs. Brood patch temperature remained essentially constant throughout the range of external air temperatures. Walters (1958) recorded brood patch temperatures of Snowy Plovers with a mercury bulb thermometer placed in a position comparable to the thermistors used in this study. His mean of 40.8° is somewhat higher than the means I obtained, but readings above 40°C were common in my study.

Both male and female Snowy Plovers incubate eggs (Walters 1958, Rittinghaus 1961). Figure 7 indicates that the duration of a parental shift is related to the external thermal environment. At cool and moderate air temperatures diurnal shifts were infrequent and seldomly detected, which explains the long periods (up to 16 hr) shown in figure 7. In hot weather the shifts were much more frequent, and at air temperatures above 40°C the shifts were less than 1 hr apart. Boyd (1972) showed that during hot weather Snowy

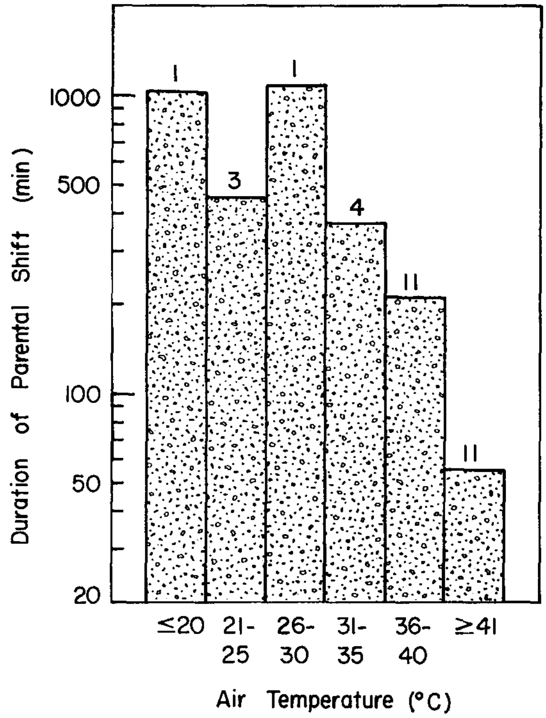

FIGURE 7. Effect of air temperature on length of periods between parental shifts. Number of observed shifts is indicated above bar.

Plovers apply moisture collected in their breast feathers from nearby pools to the egg surfaces. He reported similar behavior for Killdeer (*Charadrius vociferus*). Increases in this behavior may account for the increase in shift frequency at high air temperatures (fig. 7).

Drent (1973) concluded that such behavior as standing over the eggs and wetting the eggs with external water, is merely for adult thermoregulation and that any benefit for the eggs is coincidental. However, analysis of the temperatures at the top of the plover's eggs indicates that standing may be, at times, more effective than sitting in keeping the eggs cool. With air temperatures greater than 36°C, 53 measurements at times when adults were standing over the eggs showed a mean temperature of 39.58°C, while 63 comparable readings taken when the parents were sitting had a mean of 40.07°C. Analysis of variance indicated a significant difference between these two means ($P < 0.05$). These figures, coupled with the greater incidence of standing at higher air temperatures (fig. 6), imply that standing may be an efficient way to keep the eggs from overheating, especially when combined with egg wetting.

However, the above effect may be tempered by wind. I have shown (Purdue, in press)

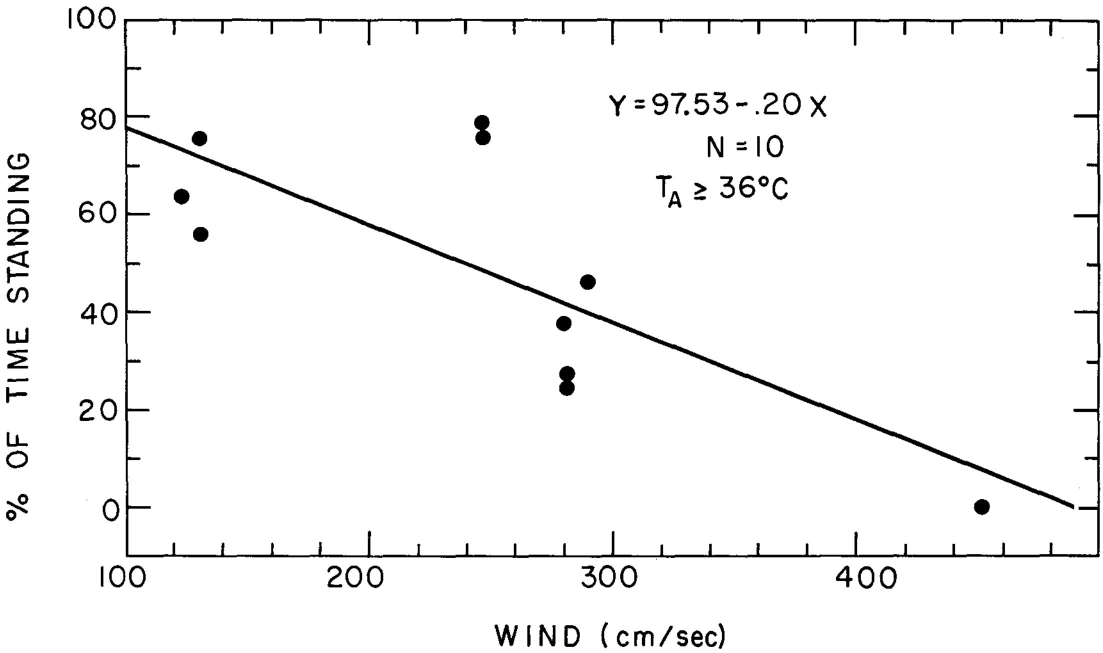

FIGURE 8. Effect of wind on standing over the nest. Regression coefficient is significantly different from zero ($P < 0.05$).

that unvegetated salt flats receive much more wind action than the surrounding grasslands. Figure 8 shows a statistically significant negative relationship between the incidence of standing over the eggs and wind speed when air temperatures are greater than 36°C. This relationship may be the result of at least three non-exclusive factors: (1) High-velocity winds carry along the surface of the ground many sand and salt particles which can be quite abrasive. (2) High wind speed would break up the boundary layer of air surrounding the eggs and at high temperatures increase the transfer of heat to the eggs. (3) Adult plovers weigh only 30–40 g and may not be able to remain standing in high wind. By sitting on the eggs during this time the parent protects the eggs from all three hazards. White-winged Doves (*Zenaida asiatica*) in the southwestern American desert, presumably with limited water available for breast wetting, sat tightly on the eggs when ambient temperatures were extremely high (Russell 1969). In both the doves and the plovers, heat from the eggs was probably transferred to the adult via the brood patch.

In conclusion, Snowy Plovers nest in areas where eggs can be exposed almost daily to lethal temperatures. The parents incubate in various ways which are finely adjusted to ambient conditions, thus maintaining a suitable thermal environment for the eggs.

SUMMARY

The thermal environment of the eggs of Snowy Plovers was measured by placing thermistors in eggs and in strategic positions around the nest. Eggs which were outside the nest and not receiving adult attention attained much higher, presumably fatal, temperatures than eggs inside the nest. Egg temperatures were positively correlated with air and surface temperatures, but thermal extremes were moderated by parental behavior.

Time spent on the nests by the adults was correlated with several interrelated factors. Nest attention increased during the last two-thirds of the incubation period and during times of high air temperature. Nest attention diminished in late afternoon, a period of peak foraging activity and moderate temperatures. The duration between shifts at the nest was reduced at high air temperatures while the amount of time spent standing rather than sitting over the nest increased. High wind speeds reduced the latter tendency.

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LITERATURE CITED

BENT, A. C. 1929. Life histories of North American shore birds. Part II. U.S. Nat. Mus. Bull. 146.

BOYD, R. L. 1972. Breeding biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. M.S. thesis, Kansas State Teachers College, Emporia.

DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Suppl. 17: 1–132.

DRENT, R. H. 1973. The natural history of incubation, p. 262–311. *In* D. S. Farner [ed.], Breeding biology of birds. Nat. Acad. Sci., Washington, D.C.

HALL, K. R. L. 1958. Observations on the nesting sites and nesting behaviour of the Kittlitz's Sandplover *Charadrius pecuarius*. Ostrich 29:113–125.

HOWELL, T. R., AND G. A. BARTHOLOMEW. 1962. Temperature regulation in the Sooty Tern *Sterna fuscata*. Ibis 104:98–105.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22.

NORTON, D. W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164–176.

PURDUE, J. R. In press. Adaptations of the Snowy Plover on the Great Salt Plains, Oklahoma. Southwest. Nat.

RITTINGHAUS, H. 1961. Der Seeregenpfeifer. A. Ziemsen Verlag, Wittenberg, Lutherstadt.

RUSSELL, S. M. 1969. Regulation of egg temperatures by incubating White-winged Doves, p. 107–112. *In* C. C. Hoff and M. L. Riedesel [eds.], Physiological systems in semiarid environments. Univ. New Mexico Press, Albuquerque.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco.

VON HAARTMAN, L. 1956. Der Einfluss der Temperatur auf den Brutrhythmus experimentell nachgewiesen. Ornis Fenn. 33:100–107.

WALTERS, J. 1958. Über de Brutflecktemperaturen bei See- und Flussregenpfeifern, *Charadrius alexandrinus* und *dubius*. Ardea 46:124–138.

WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. Science 186:107–115.

Quaternary Studies Center, Illinois State Museum, Springfield, Illinois 62706. Accepted for publication 27 May 1975.