

THE EFFECT OF EGG TEMPERATURE ON ATTENTIVENESS IN THE BELDING'S SAVANNAH SPARROW

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ABSTRACT.—We manipulated egg temperatures in nests of the Belding's Savannah Sparrow, (*Passerculus sandwichensis beldingi*), an open-nesting passerine of which only the female incubates. Females increased their attentiveness by 22.0% when we cooled their eggs and decreased their attentiveness by 28.4% when we warmed their eggs. The range of adjustment approximated the upper and lower limits of attentiveness observed for our population during one breeding season; adjustments were primarily made by changing the length of both attentive and inattentive periods. Our results indicate that these birds adjust their attentive time in direct response to fluctuations in egg temperature, independently of diurnal fluctuations in air temperature. They also support the hypothesis that attentiveness is ultimately controlled by an internal rhythm and is only modified by, but not completely explained by, responses to egg temperature. Received 14 September 1983, accepted 6 February 1984.

AVIAN egg temperature (T_e) must be controlled within narrow limits to insure proper embryological development (Lundy 1969, Romanoff and Romanoff 1972, Weinrich and Baker 1978). Many species accomplish this by continuously incubating their eggs; parents either share in the responsibility of incubation, or a nonincubating partner feeds its incubating mate (Drent 1975, Carey 1980). Other species engage in intermittent incubation by one parent. In this case, the maintenance of T_e within narrow limits is especially challenging. During daylight hours, the incubating parent (usually the female) must compensate for fluctuations in environmental temperature and also take sufficient time away from the nest to feed. This control of T_e is accomplished primarily through adjustments of attentiveness (Kendeigh 1952, White and Kinney 1974, Yom-Tov et al. 1978) and secondarily by regulation of heat transfer through the brood patch (Drent et al. 1970, Haftorn 1982).

Many studies demonstrate a correlation between attentiveness and air temperature (T_a) (Kendeigh 1952, White and Kinney 1974, Yom-Tov et al. 1978), but, because T_a and mean T_e may vary in parallel (Huggins 1941, Yom-Tov et al. 1978, Zerba and Morton 1983, Webb and King 1983), it is impossible to determine whether or not T_a influences attentiveness independently of T_e without experimentally uncoupling the two. We are not aware of any study in which this has been done.

Because the primary function of adjustments

in attentiveness is to regulate T_e , the most effective mode of regulation should be via the direct detection of and response to T_e . This is suggested by a number of investigators. For example, Drent (1972: 259) suggested that the key stimulus to guide a parent in adjusting its incubation rhythm is T_e measured at the moment the parent returns to the nest after a recess. Experimental evidence to support this hypothesis, however, is at best indirect.

Using hole nesters, von Haartman (1956) and Johnson and Cowan (1974) artificially heated nest boxes in the field to determine the influence of ambient temperatures at the nest on attentiveness. Von Haartman reported a decrease in attentiveness (sessions at the nest) with an increase in nest-box temperature on the part of his Pied Flycatchers (*Ficedula hypoleuca*), but Johnson and Cowan found no response in Crested Mynas (*Acridotheres cristatellus*). T_e was not measured and therefore not separated from T_a of the nest-box complex in either of these experiments.

White and Kinney (1974) presented indirect evidence that sensory perception of T_e through the brood patch of the incubating female is used as a feedback stimulus to control attentiveness. Working with Village Weaverbirds (*Ploceus cucullatus*), they found that anesthetation of the brood patch of incubating females increased attentiveness. They speculated that the anesthetation caused a reduction of the frequency of discharge of sensory receptors located in the skin of the brood patch, which encouraged at-

tentiveness. They also found high cooling rates of eggs within different nests to be associated with high attentiveness, implicating an influence of T_e . From a graphical analysis of attentiveness versus T_a , they found that a rectangular hyperbolic function fit their data best. This function predicted intercept T_a for zero attentiveness to be $37.0^\circ\text{C} \pm 0.6$ (95% confidence interval), which corresponded closely to their mean maximum T_e during the day ($36.7^\circ\text{C} \pm 1.5$ SD) and during the night ($36.7^\circ\text{C} \pm 1.4$ SD). From these results, White and Kinney hypothesized that 37°C corresponds to a "release temperature" of the egg, which the incubating female detects by the brood patch as a cue to leave the nest. They also argued that the detection of T_a near 37°C promotes cessation of incubation.

Recently, Zerba and Morton (1983) found this "release temperature" in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) to be relatively constant at $38.0^\circ\text{C} \pm 1.5$ SD throughout the day in an environment with large temperature fluctuations. They concluded that incubating females must be acutely sensitive to T_e .

The purpose of our study was to separate for the first time the effects of T_e from those of T_a on attentiveness in a species displaying intermittent incubation by one parent. We did this by controlling T_e in nests throughout the day, in situ, by either warming or cooling the eggs and observing responses in attentive behavior. We selected two treatment levels for our control of T_e : one near the mean minimum T_e , to approximate the normal temperature sensed by an incubating parent at the moment of its return to the nest after a recess, and the other near the mean maximum T_e , to represent the normal temperature at the moment when an incubation session stopped and recess began. Thereby we obtained direct evidence to test two hypotheses: (1) the hypothesis of Drent (1972) that birds use T_e measured at the moment of return to the nest after a recess to adjust attentiveness, and (2) the hypothesis of White and Kinney (1974) that birds use a "release temperature" of their eggs to cue departure from the nest.

MATERIALS AND METHODS

Birds and study area.—We chose the Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*), a

permanent resident of the coastal marshes of Southern California and a species in which only the female incubates, as our study species. Our study site was a salt marsh neighboring the eastern arm of Point Mugu Lagoon at the Point Mugu Naval Air Station near Oxnard, California ($34^\circ06'30''\text{N}$, $119^\circ05'\text{W}$). Male Savannah Sparrows established territories in early March, and breeding occurred from March to July. Females constructed nests just above ground level in low-profile halophytic succulents and grasses. The nests were open but shaded from direct solar radiation during most of the day. The mean clutch size was 3.2 eggs ± 0.05 (SE, $n = 356$), and the incubation period was 13.2 days ± 0.3 (SE, $n = 6$).

Egg temperature.—We measured egg temperatures with 40-gauge thermocouple wire inserted near the center of one egg in a clutch and cemented in place with a dental resin (Caulk Grip Cement, L. D. Caulk Co., Div. Dentsply Intern. Inc., Milford, Delaware). Temperatures were continuously monitored by potentiometric recorder (Linear, Model 142, Linear Instruments Corp., Irvine, California). We calibrated thermocouple and recorder output each day by comparison with a standard thermometer calibrated to the National Bureau of Standards. Temperature readings were accurate to within $\pm 0.2^\circ\text{C}$. Visual comparisons verified that chart recordings accurately represented the time that a bird arrived and departed from the nest to within 20 s.

Definitions and computations.—We defined "attentiveness" as the number of total minutes a bird incubated her eggs for a given hour, "attentive period" as the number of minutes spent on the eggs per visit to the nest, and "inattentive period" as the number of minutes spent off the eggs per recess from the nest. We computed mean T_e from the chart recordings by means of a digitizer (Hipad, Houston Instrument, Austin, Texas) and software that computed the mean T_e per hour, per day period, and per night period from 100 equally spaced temperature observations for each hour (one temperature measurement per 36 s). Therefore, a mean T_e for a 24-h period represented the mean of 2,400 temperature observations. We verified that the measurement and statistical computation of mean T_e were accurate by comparing them with manual measurements made directly from the chart recordings and with the SPSS statistical package (Nie et al. 1975). We defined the mean maximum T_e per hour as the mean of the egg temperatures taken at the end of each attentive period for a given hour. Similarly, we calculated the mean minimum T_e per hour from the beginning of each attentive period. Mean T_e per hour was taken from the U.S. Navy Weather Station less than 1 km from the study site. We also recorded air temperatures in the vegetation adjacent to nests with a shielded thermocouple.

Apparatus to manipulate egg temperature.—We designed an apparatus to deliver heated or cooled air

to the bottom of a nest just beneath the eggs. It consisted of a 15-mm-diameter, 3-m-long copper tube enclosed within an insulated 30-mm-diameter copper tube. A variable-speed fan gently forced air through the inner tube to the nest while polyethylene glycol was circulated by a refrigerated water bath (Neslab, Model RTE-8, Neslab Instruments Inc., Portsmouth, New Hampshire) through the outer tube to regulate the temperature of the air stream. We used thermocouples to monitor air-stream and water-bath temperatures. We placed the fan 20 m and the water bath 50 m from the nest to reduce motor noise at the nest.

Air velocities delivered to the bottom of the nest varied from 0 to 2 m/s while the bird was on the nest (measured with a hot wire anemometer, Model HWA-103, Thermonetics Corp., San Diego, California). During cooling treatments, we manually increased velocities to 4 m/s when the bird was off the nest by means of a variable rheostat attached to the fan motor. Smoke placed in the air stream showed that most of the air followed the path of least resistance out of the bottom and sides of the nest and not between the eggs into the nest cup. This finding was supported by the measurement of air velocities 10 mm above the eggs of less than 0.1 m/s (below background levels) at maximum fan speeds. Thermocouples placed in one typical nest cup indicated a maximum difference of 3.0°C between the ambient temperature and the temperature 10 mm above the eggs and no difference between the two temperatures at 50 mm above the eggs. This indicated that T_c was controlled primarily by conductive heat exchange between the fine-mesh nesting material and the undersurface of the eggs and not through forced convection by air currents. Because airflow into the nest cup was presumably even more restricted when the bird was on the nest (due to increased resistance to air flow and our reduction of fan speed), we assumed that air flowing into the nest contributed little to the temperature experienced by the female through the brood patch.

Experimental protocol.—Our experimental objectives were twofold. First, we attempted to describe the normal attentive pattern of our population under various conditions of weather and microhabitat by measuring T_a , T_c , and attentiveness throughout the breeding season of 1979 (27 April to 10 July) at 7 nests for 22 days. We selected three different microhabitats within our study site, which offered different conditions and vegetational types (*Salicornia virginica*, *Frankenia grandifolia*, and *Monanthocloe littoralis*) for nesting.

Second, we used these results to design an experiment to manipulate T_c in situ during the breeding season of 1980. We selected four representative nests, very similar in microhabitat (all in *Salicornia* vegetation and within a 1-ha area), time of incubation (within 20 days of each other, 8–28 June), and exposure to daily T_a . In each nest, eggs were heated,

cooled, and left untreated on alternate days from 0600 to 1800. We used data from the untreated day as our control for each nest. We varied the order of the treatments among nests to determine whether or not the sequence of treatments affected results.

An example of digitized T_c data for a typical nest on three consecutive days of control, cool, and heat treatments is shown in Fig. 1. Because the incubating female aided the heating of eggs but hindered the cooling of them, T_c on the heated day is nearly constant, whereas T_c on the cooled day is not. T_c on the cooled day continues to reflect an incubation pattern. Visual inspection of this pattern indicates that attentive periods are longer on the cooled day than on the control day.

We maintained T_c below the mean minimum T_c of the control on cooled days and above the mean maximum T_c of the control on heated days (Fig. 1). This allowed us to test our hypothesis that T_c directly affects attentive behavior, specifically the T_c at the moment when the female returns to the nest for a session (mean minimum T_c) and at the moment when she departs from the nest for a recess (mean maximum T_c , "release temperature").

RESULTS

Normal attentive pattern of the population.—Attentiveness at seven nests varied with the time of day on 22 days between 27 April and 10 July 1979 (Fig. 2A). A polynomial regression of the data predicted a minimal attentiveness of 31.9 min at 1257 (obtained by setting the derivative of attentiveness with respect to time equal to zero). Mean attentiveness during daylight hours (0500–2000) was 39.3 min \pm 0.51 (SE, $n = 383$). The mean number of attentive periods per hour was 3.4 \pm 0.08 (SE, $n = 383$).

Attentive pattern of manipulated nests.—Attentiveness at four nests on 15 days between 8 and 26 June 1980 varied with mean hourly T_a (Fig. 2B). A linear regression of the data ($y = 73.102 - 1.946x$) predicted an x -intercept (extrapolation to 0 attentiveness) at 37.6°C + 8.4, -7.8 (95% confidence interval), a temperature not significantly different from the mean maximum T_c per hour of 38.3°C ($P > 0.50$).

We manipulated T_c independently of T_a in these same four nests, giving a total of 5 cooled, 5 heated, and 15 untreated (control) days (Fig. 3). Each treatment period was continuous for 12 h (0600–1800).

Except during the heat treatment at 1000 at nest C and at 0900–1500 at nest D, females generally increased their attentiveness when eggs were cooled and decreased attentiveness when

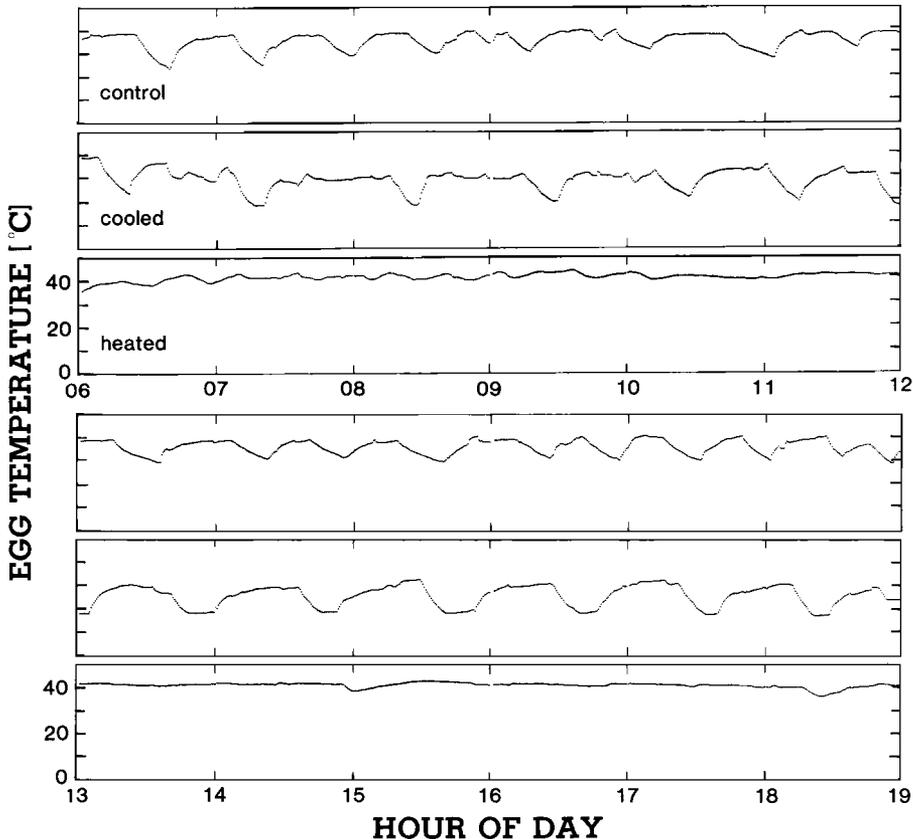


Fig. 1. Example of digitized egg-temperature data from a manipulated nest from 0600 to 1900 Pacific Standard Time (PST) on a control day (16/6/80), cooled day (17/6/80), and heated day (18/6/80).

eggs were heated, relative to control days (Fig. 3). The aberrant increase in attentiveness between 0900 and 1500 during the heat treatment at nest D coincided with the onset of high winds (gusting to 46 km/h). We know that the female increased her attentiveness at the nest during the windy period, but we cannot be certain that she was actually incubating her eggs, because T_e was held constant during heat treatments (cf. Fig. 1). We also collected data on an "untreated" nest on this same day of high winds, however, and found a dramatic increase in incubation as indicated by T_e recordings (data not shown).

The reason for this increase in attentiveness with the onset of high winds is not clear. It is unlikely that the incubating female was attempting to prevent egg desiccation. Tracy and Sotherland (1979) have shown that movement of air across the surface of an egg will not sig-

nificantly increase rates of water loss, and Walsberg (1983) demonstrated that birds do not respond to manipulated nest humidities. Possibly, the female was attempting to compensate for an increase in the cooling rate of eggs associated with high winds. We tested this by artificially ventilating three eggs in a nest, in situ, with a 10 m/s (36 km/h) air velocity. Cooling rates of the eggs (from 40.0°C down to 35.0°C, with a T_a of 26.0°C) increased from 2.2°C/min to 9.8°C/min. Cooling rate was not a factor on the heated day of Fig. 3D, however, because we continuously held eggs at or above 38°C. We also observed that the female had extreme difficulty in flight navigation during the windy period, and it may be that she remained on her nest to conserve energy (cf. Tucker 1971).

Figure 4A shows combined data for attentiveness and mean T_e for heated, cooled, and untreated days. A Bartlett's test of homogeneity

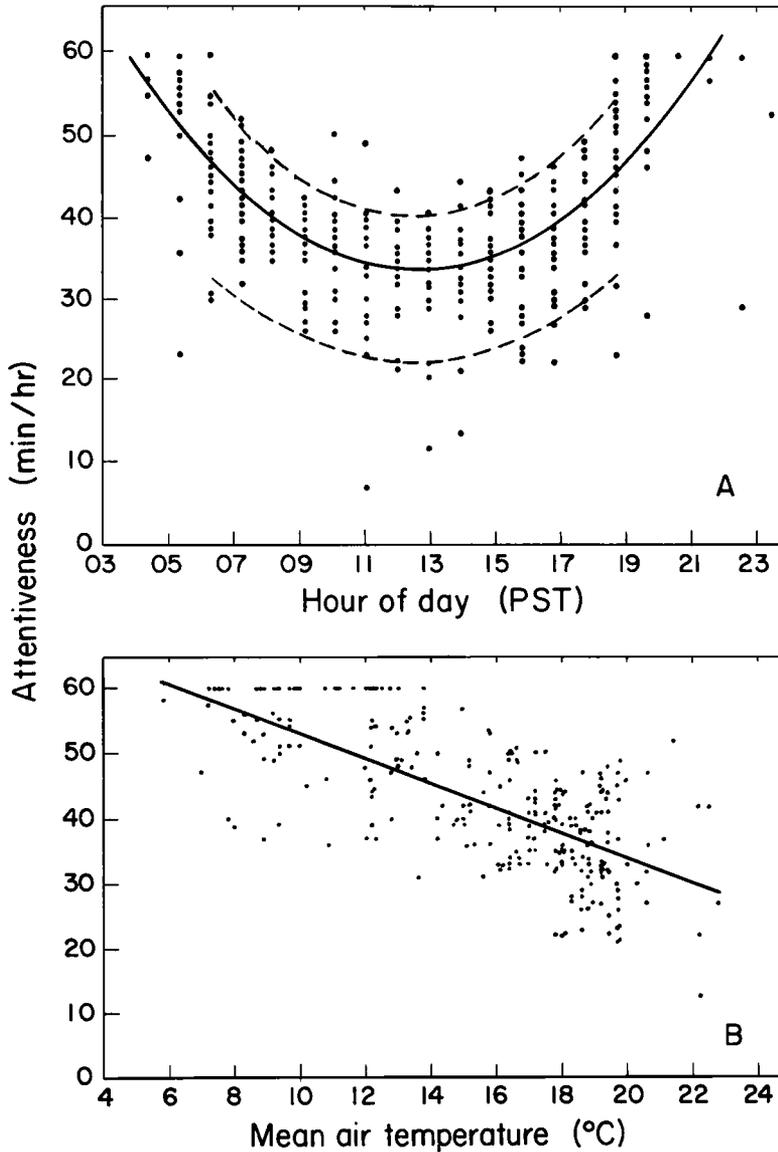


Fig. 2. (A) Attentiveness during daylight hours (0500–2000, PST) at seven nests for 22 days and 383 h during the breeding season of 1979. Polynomial regression, $y = 85.87 - 8.34 \times 10^{-2}x + 3.22 \times 10^{-5}x^2$, $F = 155.67$, $r^2 = 0.45$, $n = 383$. Dashed lines represent a range of attentiveness extending 22.0% higher and 28.4% lower than the polynomial regression, from 0600 to 1800. (B) Attentiveness versus mean air temperature during daylight hours at four nests for 15 days and 270 h, between 8 and 26 June 1980. Linear regression, $y = 73.102 - 1.946x$, $r^2 = 0.51$, $n = 270$, $P < 0.001$.

of variances between the three treatments (Sokal and Rohlf 1969: 370) indicated a significant heteroscedasticity ($\chi^2 = 73.23$, $P < 0.001$). Therefore, we tested the significance of the treatments nonparametrically. A Mann-Whitney U -test indicated a significant increase in

attentiveness on cooled days ($t = 22.50$, $P < 0.001$) and significant decrease in attentiveness on heated days ($t = 7.30$, $P < 0.001$) relative to untreated (control) days. Furthermore, a Kruskal-Wallis test for each of the 12 h of treatment indicated that the treatments differed signifi-

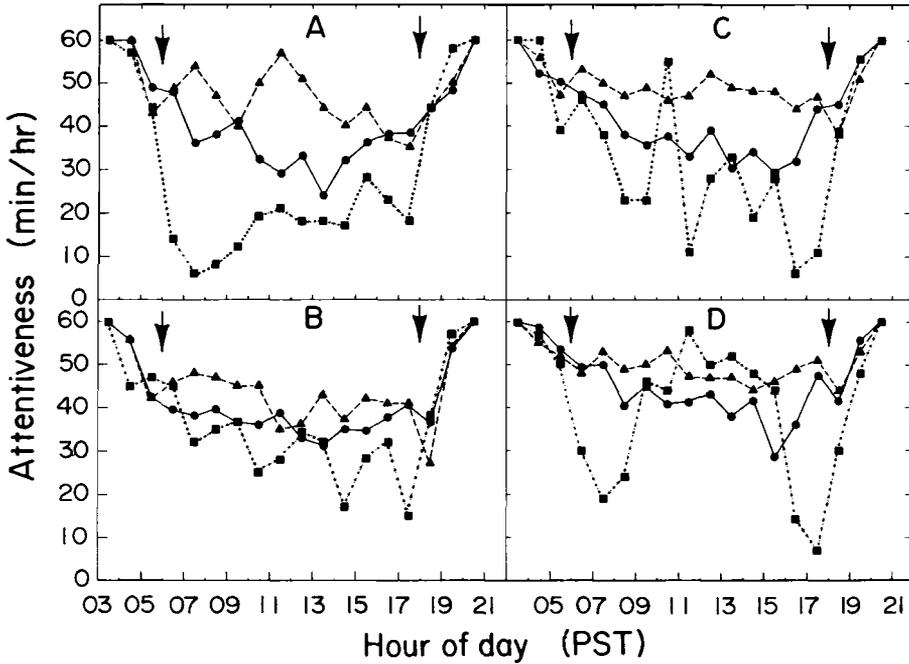


Fig. 3. Attentiveness versus hour of the day for four birds, labeled A, B, C, and D, and three treatments, labeled heated (■), cooled (▲), and untreated (●) days.

cantly at all hours (range from $\chi^2 = 7.04$ to 16.67, $P < 0.05$ to $P < 0.001$).

The mean T_e was $30.6^\circ\text{C} \pm 0.39$ (SE, $n = 60$) for cooled days, $35.5^\circ\text{C} \pm 0.15$ ($n = 180$) for control days, and $40.4^\circ\text{C} \pm 0.17$ ($n = 60$) for heated days (Fig. 4A). Egg temperatures during manipulation were within the range normally experienced by the incubating female and approximated the upper and lower temperature limits experienced upon departure from (mean maximum T_e per hour = $38.3^\circ\text{C} \pm 0.14$ SE, $n = 178$) and arrival at the nest (mean minimum T_e per hour = $31.1^\circ\text{C} \pm 0.24$, $n = 178$). The mean T_e of 40.4°C on heated days was close to the surface temperature of the brood patch of incubating females ($40.2^\circ\text{C} \pm 0.42$ SE, $n = 8$).

On cooled days, the mean minimum T_e per hour was $23.9^\circ\text{C} \pm 0.59$ (SE, $n = 58$), and the mean maximum T_e was $33.3^\circ\text{C} \pm 0.45$ ($n = 56$). On heated days, the mean minimum T_e was $39.6^\circ\text{C} \pm 0.21$ ($n = 55$), and the mean maximum T_e was $40.7^\circ\text{C} \pm 0.17$ ($n = 54$). Therefore, T_e perceived by the incubating female at the moment of return to the nest after a recess averaged 7.2°C below the control on cooled days and

8.5°C above the control on heated days. Furthermore, when our birds returned to the nest on heated days they immediately experienced a T_e at or above their "release temperature" of 38.3°C (mean maximum T_e of the control); at no time, however, did they experience T_e as high as a "release temperature" on cooled days.

Because the treatments were on different days, our data from untreated days represented an adequate control only if T_a was similar among days. Fortunately, ocean air currents ameliorated temperature fluctuations at our study site (Fig. 4B). A two-way analysis of variance, with treatments and hour of the day as covariates, indicated that T_a did not differ significantly between days ($F = 1.98$, $P > 0.1$).

Attentive and inattentive periods at control nests.—Out of 11 nests measured during the breeding seasons of 1979 and 1980, correlation analysis (Pearson product-moment, Nie et al. 1975: 280) of attentive and inattentive periods versus mean hourly T_a between 0600 and 1800 indicated that there was a negative correlation between attentive period and T_a ($P \leq 0.05$) at 7 nests and a positive correlation between inat-

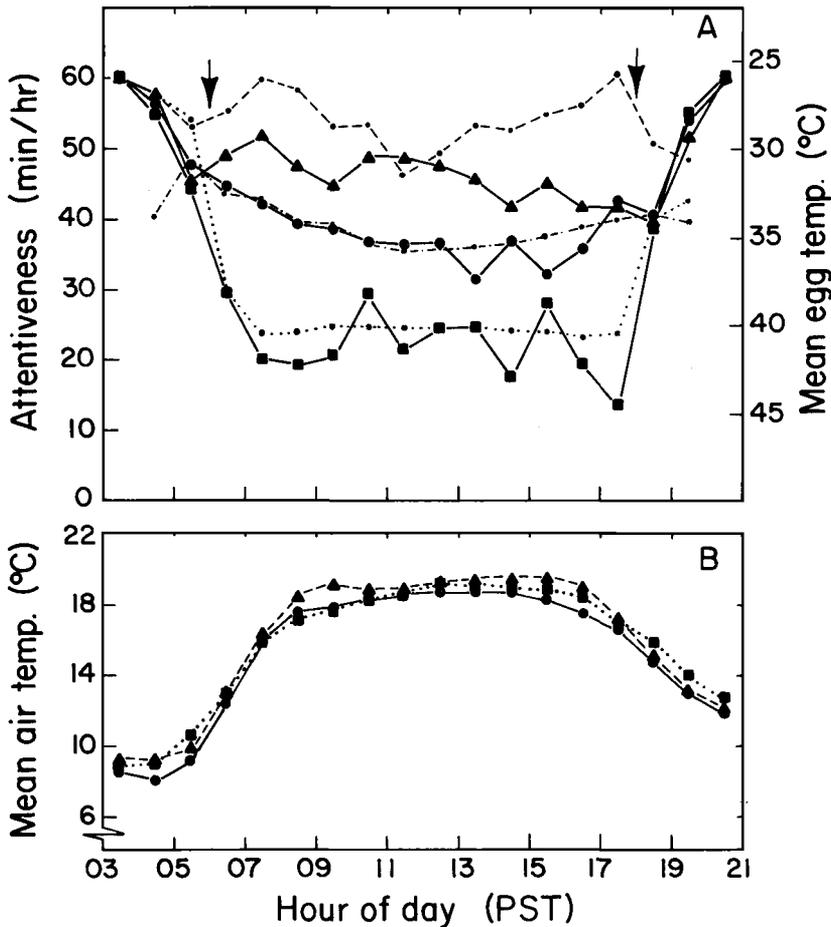


Fig. 4. (A) Attentiveness versus hour of the day for heated (■), cooled (▲), and untreated (●) days, with associated mean egg temperatures on heated (•····•), cooled (•—•), and untreated (•····•) days. (B) Air temperature versus hour of the day for heated (■), cooled (▲), and untreated (●) days.

tentive period and T_a ($P \leq 0.05$) at 8 nests (data not shown). Combined data for all 11 nests gave a regression equation of $y = 20.86 - 0.496x$ ($n = 1,390$, $r = -0.13$, $P < 0.001$) for attentive period versus T_a and $y = 3.38 + 0.257x$ ($n = 1,409$, $r = 0.08$, $P < 0.002$) for inattentive period versus T_a . Considering the high variability in attentive and inattentive periods within and among individual birds in a population, as observed here and by others (Kendeigh 1952, Weeden 1966, Haftorn 1979), the significance of these correlations is probably real.

Attentive and inattentive periods at manipulated nests.—High variability in comparing single observations of attentive and inattentive pe-

riods versus T_a is typical, and grouping data to enhance patterns that are present is common (Kluyver 1950, Kendeigh 1952, Weeden 1966, Haftorn 1979). We have employed such a method by grouping our data into T_a ranges of 1.0°C intervals so that each point represents the mean attentive or inattentive period for our four manipulated nests in each temperature range (Fig. 5).

On control days, the attentive period correlated negatively with T_a , whereas the inattentive period displayed a biphasic relationship (Fig. 5). At T_a below 13.5°C , inattentive periods decreased with increasing T_a , whereas at T_a above 13.5°C the pattern was reversed. Solving

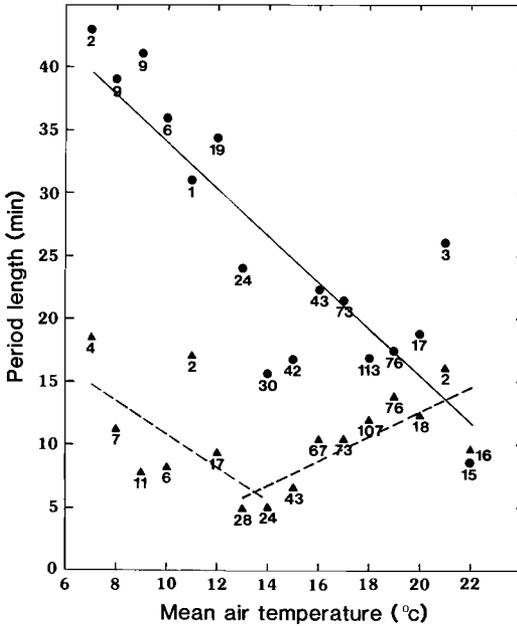


Fig. 5. Mean attentive (●) and inattentive (▲) periods versus mean air temperature (grouped into 1.0°C intervals) for manipulated nests on untreated days. Numbers under each data point represent the number of observations for each mean value. Linear regression for attentive period versus mean T_a , $y = 52.75 - 1.86x$ ($r^2 = 0.72$, $n = 16$, $P < 0.001$); for inattentive period versus mean T_a from 7°C to 14°C, $y = 24.08 - 1.32x$ ($r^2 = 0.41$, $n = 8$, $0.10 < P > 0.05$); for inattentive period versus mean T_a from 13°C to 22°C, $y = -6.85 + 0.97x$ ($r^2 = 0.63$, $n = 10$, $P < 0.01$).

the equations for the point of intersection gave an inattentive period of 6.2 min and a T_a of 13.5°C. This biphasic pattern might be explained by the fact that T_a below 13.5°C occurred only during early morning hours when the birds were first coming off their nest after a long night. These longer inattentive periods during early morning hours may be in response to an intensified hunger drive.

Kendeigh (1952: 41) found a similar pattern in the House Wren (*Troglodytes aedon*) when he plotted the daily average inattentive period against daily average T_a . He found inattentive periods to be negatively related to T_a below 13°C but positively related to T_a above 13°C. He attributed this increase in inattentive period with T_a below 13°C to an increase in the need for food and, thus, an increase in the time required to search for food on cool days.

In Fig. 6A, attentive periods are compared with T_a on control, cooled, and heated days. A comparison of the regression equation for cooled days with that for control days indicated that their slopes were the same ($t = 0.36$, $P > 0.50$) but their elevations were different ($t = 4.43$, $P < 0.001$). A similar comparison between heated days and control days also indicated equal slopes ($t = 0.29$, $P > 0.50$) and unequal elevations ($t = 5.17$, $P < 0.001$). Therefore, it appears that the length of attentive periods increased on cooled days but decreased on heated days. This suggests that birds adjusted attentive periods in a direct response to T_e independent of the influence of T_a . Furthermore, it appears that even on cooled and heated days the negative correlation between attentive period and T_a persisted.

In Fig. 6B, inattentive periods are compared with T_a for control, cooled, and heated days. A comparison of the regression equation for heated days with that of control days (between T_a of 13°C to 22°C) indicated that their slopes were the same ($t = 0.09$, $P > 0.50$) but their elevations were different ($t = 9.00$, $P < 0.001$). A similar comparison between cooled days and control days (between T_a of 7°C to 14°C) indicated equal slopes ($t = 1.42$, $P > 0.10$) and equal elevations ($t = 1.06$, $P > 0.20$). Females lengthened inattentive periods on heated days relative to control days, and a positive correlation between inattentive periods and T_a persisted. In contrast, on cooled days inattentive periods were shortened, but only at T_a greater than 18°C. The reason for no shift in inattentiveness at T_a below 18°C is not apparent.

DISCUSSION

Female Savannah Sparrows consistently responded to cooled eggs by increasing attentiveness and to heated eggs by decreasing attentiveness, relative to control days. Attentiveness on control and heated days tracked T_e throughout the day, whereas attentiveness on cooled days followed T_e only during the morning hours (Fig. 4A). This may reflect an accumulated energy drain on the incubating parent on cooled days, which results in an increase in foraging time (decrease in attentiveness) after midday. Haftorn (1982) shows that eggs artificially cooled under field conditions cause the body temperature of an incubating female to decline, and Biebach (1979)

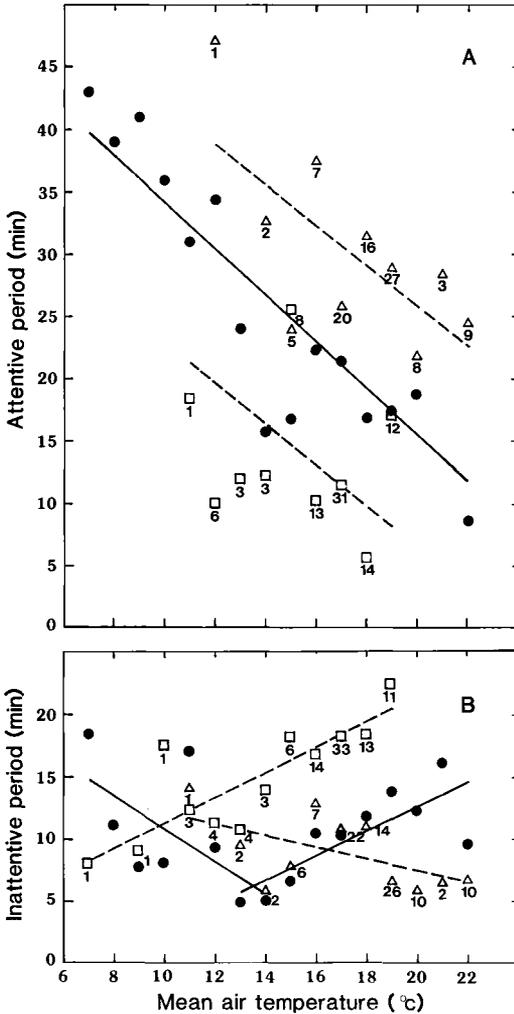


Fig. 6. (A) Attentive periods and (B) inattentive periods versus mean air temperature (grouped into 1.0°C intervals) for manipulated nests on heated (\square), cooled (Δ), and untreated (\bullet) days. Numbers under each data point represent the number of observations for each mean value. Numbers and linear regressions for control data are the same as in Fig. 5. (A) Linear regression for attentive period versus mean T_a on heated days, $y = 39.70 - 1.68x$ ($r^2 = 0.40$, $n = 10$, $P < 0.05$) and cooled days, $y = 58.29 - 1.62x$, ($r^2 = 0.47$, $n = 10$, $P < 0.05$). (B) Linear regression for inattentive period versus mean T_a on heated days, $y = 1.27 + 1.00x$, ($r^2 = 0.70$, $n = 12$, $P < 0.001$) and cooled days, $y = 17.01 - 0.48x$ ($r^2 = 0.33$, $n = 11$, $0.10 < P > 0.05$).

and Vleck (1981) show that eggs cooled in the laboratory cause energy requirements for incubating birds to increase.

An increase in mean T_e of 4.9°C on heated

days reduced attentiveness by $28.4\% \pm 2.31$ (SE, $n = 60$), whereas a decrease in mean T_e of 4.9°C on cooled days increased attentiveness by $22.0\% \pm 0.98$ ($n = 60$). These adjustments were primarily made by decreasing or increasing both attentive and inattentive periods (Fig. 6).

Our results provide the first direct evidence that T_e influences attentiveness independently of T_a in an open-nesting passerine. In addition, they indicate that T_e is not the only factor controlling attentiveness. At no time did a bird discontinue incubation in response to heating or continuously incubate in response to cooling of the eggs.

With the Village Weaverbird, White and Kinney (1974) found intercept T_a for zero attentiveness to be $37.0^\circ\text{C} \pm 0.6$ (95% confidence interval) and the mean maximum T_e to be $36.7^\circ\text{C} \pm 1.5$ (SD). They hypothesize that when an incubating female returns to the nest, she warms her eggs until a "release temperature" (ca. 37°C) is reached; this is detected by sensory receptors in the brood patch, cueing departure. Our data do not support this hypothesis. Our corresponding intercept T_a for zero attentiveness and mean maximum T_e were $37.6^\circ\text{C} (\pm 0.8)$ and $38.3^\circ\text{C} (\pm 1.9)$, respectively. In our heat treatment, we continuously held T_e at or above this "release temperature" (ca. 38°C), and yet the birds continued to incubate for some period, albeit 28.4% less intensively (Fig. 4A). Conversely, on cooled days we continuously held T_e several degrees below this "release temperature" of 38°C , yet the birds did not continuously incubate but simply increased attentiveness by 22.0%.

These results are not surprising when compared with those of experiments in which T_e is manipulated in dual-sex, continuous incubators. For example, in one experiment with the Ringed Turtle Dove (*Streptopelia risoria*), where the normal range in T_e is $38\text{--}39^\circ\text{C}$, Franks (1967) controlled T_e at -3 to 8°C for 39 h and in another experiment at 46°C for 13 days; in both cases the doves continued to incubate. As in our experiment, this indicates that sensing of T_e by the brood patch of an incubating female is not the immediate cause of the incubation rhythm.

Yom-Tov et al. (1978) found in the Dead Sea Sparrow (*Passer moabiticus*) that, at T_e and T_a greater than 36°C (mean T_e was 33.7°C , so 36°C is probably close to the "release temperature" for this species, although this number is not

given), attentiveness did not go to zero, as White and Kinney's model (1974) predicts, but abruptly increased. They attributed this increase in attentiveness by the female to a mechanism to avoid the overheating of eggs under conditions of high T_e and suggested that this is probably an adaptive behavior common in desert habitats, where T_e can reach 45°C or more at midday. When our birds were presented with T_e above their "release temperature" of 38°C, attentiveness did not increase but diminished by 28.4%. Unlike the Dead Sea Sparrow, however, our birds never experience T_e greater than 37°C (de Violini 1975) during the breeding season and therefore have probably not developed a response to avoid the overheating of their eggs.

Kendeigh (1952: 87) proposed that the rhythm of incubation is caused by an alternation between the drive to incubate and the drive to feed. He suggested that hunger contractions in the proventriculus of the Song Sparrow (*Melospiza melodia*) and House Wren furnish the primary stimulus to terminate the attentive period and initiate a search for food. It is implied that once this appetite is satiated, the drive to incubate would take precedence, and the bird would return to the nest to begin another attentive bout. If this were true in our experiment, one would expect the energy demand (cf. Biebach 1979 and Vleck 1981), and therefore the hunger drive, to intensify on days when eggs were cooled, leading to a shortening of attentive periods. This was not the case, as seen in Fig. 6A. Instead, attentive periods lengthened on cooled days, evidently in direct response to T_e .

Johnson and Cowan (1974) showed that the Crested Myna, a tropical hole nester introduced into Vancouver, British Columbia from Southeast Asia in 1897, failed to adjust its attentive rhythm adequately to the 11°C cooler breeding climate in Vancouver. This resulted in poor nest attentiveness, low incubation temperatures, and a reduction of hatching success from 98% (Myna of West Bengal) to 61%. This reduction in hatching success was overcome by heating nest boxes so they were not allowed to go below 28°C or by allowing the closely related Starling (*Sturnus vulgaris*, daylight attentiveness of 77% as opposed to 47% for the Myna) to incubate the eggs.

Experiments such as this indicate to us that the attentive pattern of a species is ultimately

controlled by an internal rhythm (cf. Haftorn 1979, 1981). Therefore, attentive patterns can be modified by, but not completely explained by, responses to T_e or T_a . Furthermore, it appears that adjustments to these external stimuli are limited to a defined range by this internal rhythm. For example, in our experiment, when we heated the eggs to maintain T_e at a level that theoretically required no incubation for development (ca. 40°C), attentiveness did not go to zero but was reduced by 28.4%. Similarly, when we cooled the eggs to maintain a T_e that theoretically required continuous incubation for development (ca. 30°C), attentiveness did not become continuous but increased by 22.0%. This suggests that the range delimited by the internal rhythm controlling attentiveness in our birds was from 28.4% below to 22.0% above the mean attentive rhythm of our population. To test this hypothesis, we plotted this range around the polynomial regression describing the attentive patterns against time of day for our population (Fig. 2A). We believe it is no accident that this range closely approximates the observed upper and lower attentive limits of the population. Furthermore, we believe it is no accident that shifts in attentive and inattentive periods in response to manipulated T_e are made in such a way that slopes of period versus T_a parallel control days (Fig. 6).

CONCLUSIONS

It appears that female Savannah Sparrows adjust their attentive rhythm in direct response to egg temperature, independently of diurnal fluctuations in air temperature. These adjustments are primarily made by changing the length of both attentive and inattentive periods. It also appears that this response to egg temperature does not cause the attentive rhythm, because when egg temperature is held constant at or above a "release temperature" of 38°C the attentive rhythm continues. It appears that the rhythm of attentiveness is ultimately controlled by an internally regulated oscillation and that sensory perception of egg temperature only modifies the rhythm of attentiveness. Furthermore, the modification of the attentive rhythm in response to egg temperature is limited to a certain range, which approximates the upper and lower attentive times observed for the population under natural conditions.

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