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DYNAMICS OF INCUBATION IN MOUNTAIN WHITE-CROWNED SPARROWS

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ABSTRACT.—The egg temperature (T_{egg}) of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) was measured throughout incubation and under natural variations in environmental conditions at high altitude. Information on T_{egg} , air temperature (T_a), nest placement and attentiveness patterns was integrated in order to elucidate adaptive forms of incubation behavior.

Despite wide daily variations in ambient conditions, incubating females were able to maintain mean T_{egg} between 34 and 38°C. Large oscillations in T_{egg} (17.8–43.0°C) occurred when females were foraging, especially during early morning and late afternoon when T_a s were low. Apparently low and fluctuating temperatures were not detrimental to embryo development. High T_{egg} s did not occur because females prevented exposure of eggs to solar heating by remaining on the nest during critical periods. Mean T_{egg} was significantly higher in ground than in aerial nests. Habitat availability seemed to be of major importance for selection of nest height. Orientation of nests with respect to the vegetational mass in which they were built was non-random and was probably related to prevailing winds or to sun exposure.

To assure hatching, parent birds must regulate the temperature of their eggs under conditions that are often highly variable and thermally stressful. Parental behaviors during incubation must therefore be highly restricted in order to maintain thermal conditions appropriate for embryonic development. Hence, selective forces are focused on such behaviors, and studies of thermal conditions of nests and eggs, coupled with simultaneously gathered data on patterns of parental attentiveness, should enlarge our understanding of avian incubation.

In early studies of egg temperature (T_{egg}) during incubation, measurements were short-term and were not made under conditions representative of natural variation in environmental conditions. These published data tend to portray incubation as a process wherein T_{egg} is rather constant throughout and the same among species (Huggins 1941, Irving and Krog 1956, Drent 1970, 1975). This image was enforced by data, derived primarily from domestic fowl, showing the importance of a constant optimum T_{egg} to development and hatching success (Romanoff and Romanoff 1949, Lundy 1969).

This concept is changing, stimulated by recent advances in technical expertise as well as the realization that the egg, together with the incubating bird with its nest and clutch, can be viewed as self-contained systems that lend themselves to precise measurement and modelling (Kashkin 1961, Calder and Booser 1973, Ricklefs 1974, Mertens 1977a, b, Walsberg and King 1978a, b, Carey 1980). Newer studies indicate that embryos of many birds experience wide ranges in temperature during their development and are resistant to chilling but rather susceptible to overheating. Adaptation to chilling is evident in that conductance of the eggshell to water vapor is low in such species (Rahn et al. 1977); although development may be arrested during cold spells, successful hatching occurs (Matthews 1954, Spellerberg 1969, Boersma and Wheelwright 1979, Wheelwright and Boersma 1979, Vleck and Kenagy 1980). Adaptation to heat stress involves marked adjustments in parental attentiveness, which include such responses as shading eggs with body and wings (Howell and Bartholomew 1962), incubating continuously (Russell 1969), or by soaking eggs with water

carried in breast feathers (Yom-Tov et al. 1978, Howell 1979). Nest location and microclimate may also help to protect embryos from exposure to temperature extremes and reduce thermal stress to the attending parent (Howell and Dawson 1954, Calder 1973, Walsberg and King 1978a, b, Schaefer 1980, Verbeek 1981, Vleck 1981).

Additional evidence of adaptive reproductive performance should be forthcoming when avian incubation is studied at locations, such as high altitude, where weather conditions fluctuate markedly and unpredictably. For this reason we chose to study the dynamics of incubation in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), a migratory finch that breeds in high mountain meadows of the Sierra Nevada of California. Throughout their nesting season, large daily oscillations in temperature, wind, precipitation, and insolation often occur. Air temperature (T_a) is usually near freezing at night, brisk cold winds and storms are common, and solar radiation in the daytime can be intense. At the beginning of their nesting season, most of the ground is often covered with snow, and vegetation is sparse. Females must select nest sites, subsequently protect eggs from freezing at night and overheating during the day, as well as shelter them from wind and precipitation. These conditions undoubtedly provide strong selective pressure for adaptive modifications of parental behaviors as well as embryo biochemistry.

MATERIALS AND METHODS

STUDY AREA

Egg temperatures were measured during the summers of 1979 and 1980 in the Sierra Nevada at Tioga Pass, Mono County, California. The study area, used since 1968, lies just outside the eastern boundary of Yosemite National Park at 3,000 m elevation. Willows (*Salix* spp.) cover approximately 60% of the subalpine meadows in the area and are used for nest sites by *Z. l. oriantha*, as are small stands of Jeffrey pine (*Pinus jeffreyi*, Morton 1978). Remaining areas in the meadows are covered with grasses, sedges and flowering annuals. Large annual variations in snowpack occur at Tioga Pass, strongly affecting the timing of reproduction and the conditions in which these sparrows nest (Morton et al. 1972, Morton 1976, 1977, 1978).

EGG AND AIR TEMPERATURES

Copper-constantan (36 ga) thermocouples were used to record T_{egg} at 12 nests. These were soldered to a heavier gauge wire for connection

to the thermometer at a suitable distance from the nest to minimize disturbance when recording equipment was checked. After a small hole was drilled in the egg, a thermocouple was inserted to the egg center and quick-setting epoxy glue was used to seal the hole and to attach a small portion of the wire to the eggshell. Leads were threaded through the nest bottom and left slack enough to allow egg turning and lateral movement of eggs within the nest. Thermocouple leads were camouflaged in the vegetation, a particularly important technique when only a single egg was present because females are most likely to abandon at the onset of the laying period. Artificial eggs were always traded for natural eggs while thermocouples were being inserted (about 30 min) to prevent desertion. Artificial eggs were made by filling silicone molds of natural eggs with an elastomer silastic (Dow-Corning medical grade 382). Silastic eggs were then painted with a non-toxic acrylic paint to resemble the original egg color and pattern of pigmentation.

Thermocouples were inserted to centers of freshly-laid eggs two to four hours after laying and into viable embryos ranging from Day 1 to 10 of incubation. Exact ages of embryos were easily obtained because most nests were discovered before or on the day the first egg was laid. In a few cases when a complete clutch was discovered, the age of an embryo was later calculated by counting back from time of hatching, using an incubation period of 12 days. Embryonic development was arrested in most cases once the thermocouple was inserted, but some embryos remained viable for up to a week. In most cases an individual egg was not monitored for more than a three-day period.

T_{egg} was read with a Bailey thermometer (Bat-12 microprobe) and recorded constantly on a single-pen Esterline Angus miniservo strip-chart recorder (Model MS 411 BB). All inputs from one nest were handled by one thermometer and recorder. Two temperature monitoring setups were used continuously during the nesting season. In one case, temperatures were recorded simultaneously from two eggs in the same clutch to determine intra-clutch differences between T_{egg} . Data on T_{egg} used for analysis were taken at 3-min intervals from the recorder charts.

T_a near nests was measured continuously on a Friez or Weather Instrument hygrothermograph placed in the shade approximately 1 m from the nest site. T_a also was read directly from a YSI telethermometer for verification of these temperatures. Other environmental conditions such as cloud cover, snow cover, wind direction and precipitation were logged daily in a field journal.

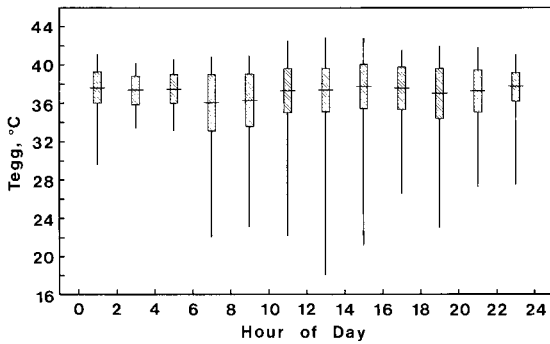


FIGURE 1. Mean egg temperature (horizontal lines) per two-hour time interval for all days of incubation. Bars denote standard deviation and vertical lines indicate the range. Temperatures were taken every three minutes. Total number of measurements from eight nests equals 17,267.

INCUBATION BEHAVIOR AND DIRECT OBSERVATIONS

Observations during incubation were made from blinds within 2 m of the nest. Behaviors such as shading of eggs, egg turning, nest maintenance, panting, body orientation, and feeding bouts were recorded and related directly to T_{egg} and environmental conditions.

Times of sunrise and sunset at the study area were obtained by direct observation. An index of exposure to solar heat loads on clear days was made by estimating every half hour the percent of the nest interior at egg height exposed directly to sun. Nest orientations were determined by compass readings taken from the center of the vegetational mass in which the nest was built. Nest orientation data were analyzed by statistical methods as outlined in Batschelet (1965). The Rayleigh Test, a statistical test of randomness, was used to determine whether the sample concentration was due to chance variation.

Data were analyzed using personal programs and SPSS (Nie et al. 1975) and BMDP (Brown 1977) statistical packages. Alpha level for tests of significance in all cases was 0.05.

RESULTS AND DISCUSSION

EGG TEMPERATURE PATTERN THROUGHOUT INCUBATION

Overall mean T_{egg} throughout incubation for eight nests when T_{egg} was taken at 3-min intervals was 37.3°C, (SD = 2.3), based on 17,267 measurements. Huggins (1941), Irving and Krog (1956), Kendeigh (1963), El-Wailly (1966), Drent (1972, 1975), and Haftorn (1978, 1979) found similar mean T_{egg} s for passerines.

Throughout incubation, mean T_{egg} was remarkably constant (between 36 and 38°C) and was largely independent of time of day (Fig. 1). Constancy in mean T_{egg} is presumably

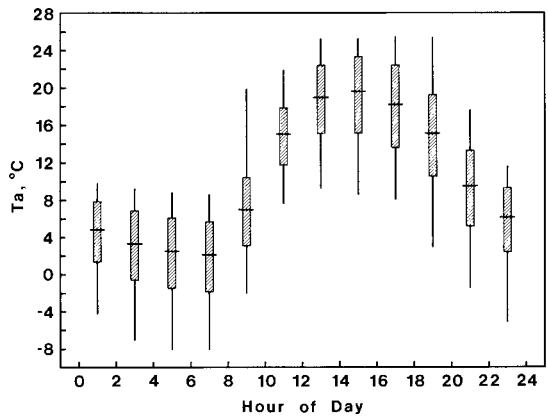


FIGURE 2. Relationship of mean air temperature (horizontal lines) to time of day from 13 June to 11 August 1980 at Tioga Pass, Mono County, California. Bars denote standard deviations and vertical lines indicate the range.

achieved by the female's pattern of attentiveness. Although mean T_{egg} remained relatively constant, actual egg temperature during the day ranged from 17.8 to 43.0°C. Most of the variation in T_{egg} occurred because low T_{a} s (Fig. 2) often coincided with times when incubating females were away foraging.

In a typical pattern over a 24-h period, T_{egg} remained relatively constant from the time when the female ended her daily activities, about 20:30, until the start of her next active day, about 6:00 (Fig. 3, upper). Nocturnal variations in T_{egg} presumably reflect adjustments in the female's posture and the position of the egg in relationship to her brood patch. During the females' early morning and late afternoon feeding bouts, large diurnal variations in T_{egg} occurred. When females left eggs untended in the cold predawn hours, T_{egg} dropped rapidly. Oscillations in T_{egg} were as much as 18°C or more within the span of a few minutes (Fig. 3, upper and lower). As T_{a} and sun exposure of the nest increased, T_{egg} fluctuations decreased in magnitude. When nests were exposed to direct sun, females usually stayed on them, presumably to prevent exposure of eggs to solar heating (e.g., Fig. 3, upper, between 10:00 and 11:00).

However, nests were sometimes left untended when exposed to direct sun, at which times eggs became warmer than the ambient temperature. Depending on T_{a} , T_{egg} increased when females were off their nests and eggs were exposed to direct sun. When T_{a} s ranged between 16–20°C, T_{egg} increased at the rate of 0.44°C/min, SD = 0.27. At T_{a} s of 21–25°C, T_{egg} increase was 0.68°C/min, SD = 0.33. (Examples of this effect can be seen in Fig. 3, lower: between 13:45 and 15:45 the female left the nest twice on foraging trips. Both times T_{egg} in-

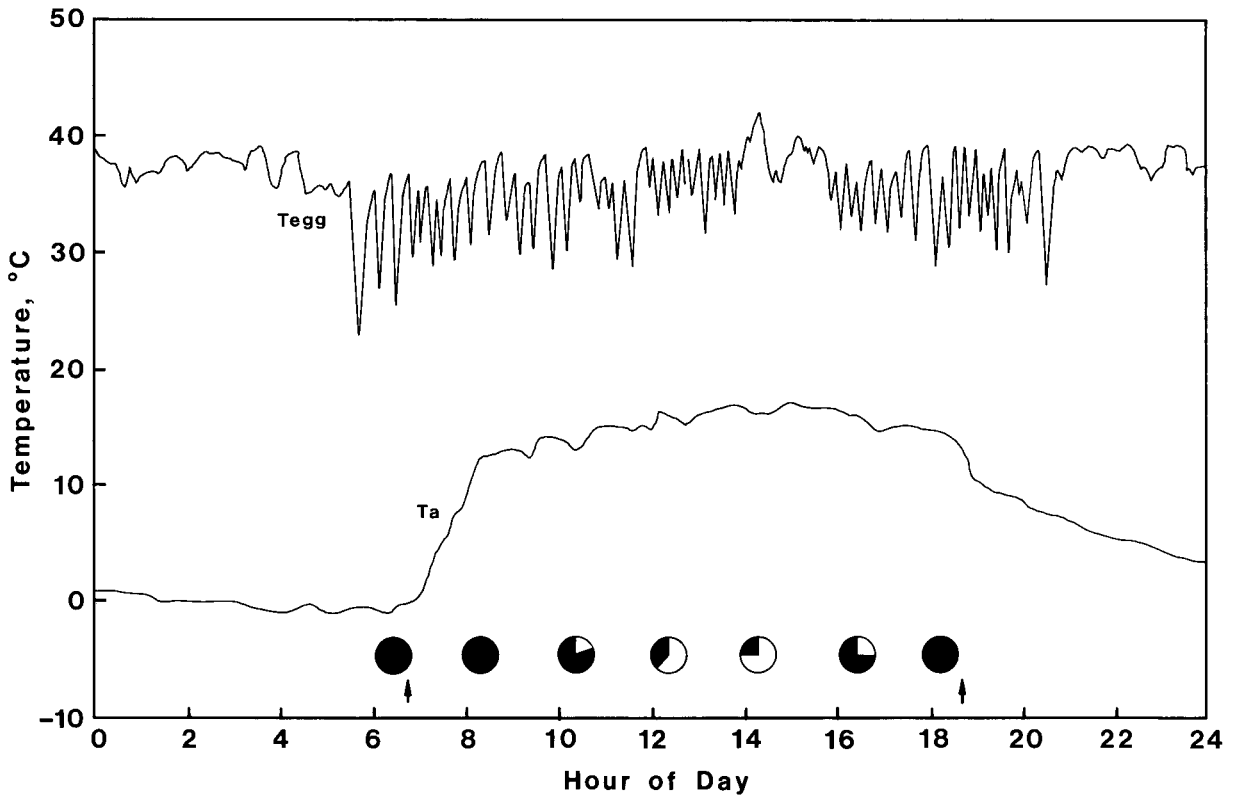
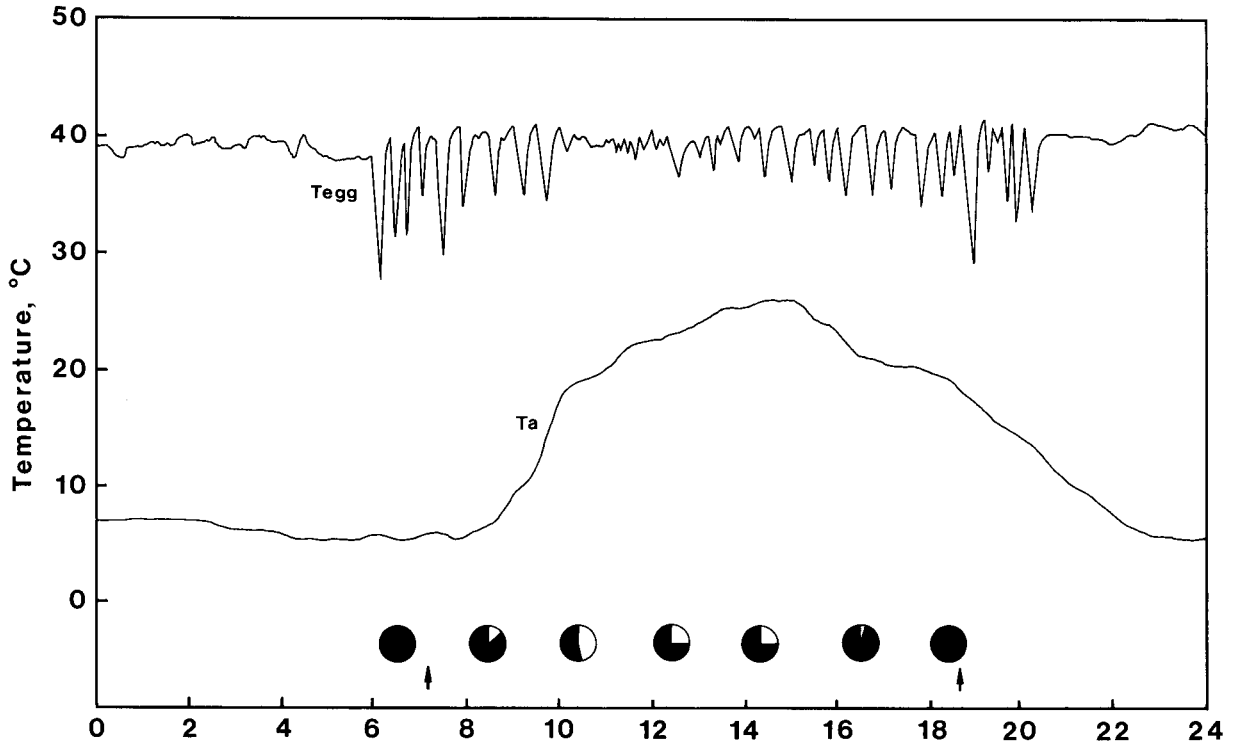


FIGURE 3. Egg temperature (T_{egg}) and air temperature (T_a) patterns from two different individuals during 24-h periods. Arrows indicate times of sunrise and sunset. White portions of circles represent the amount of nest interior exposed to sun.

TABLE 1. Egg temperatures as percent of time during active day and night rest periods.

Temperature interval, °C	Percent occurrence	
	Active day	Night rest
16-18	0.01	0.00
18-20	0.02	0.00
20-22	0.03	0.00
22-24	0.10	0.00
24-26	0.19	0.00
26-28	0.26	0.01
28-30	0.72	0.04
30-32	2.27	0.04
32-34	6.59	1.06
34-36	16.13	8.63
36-38	32.59	46.11
38-40	33.11	38.83
40-42	7.90	5.28
42-44	0.09	0.00

creased while she was off the nest and did not decrease until she returned.) Females sitting on nests exposed to direct sun often panted heavily.

Despite large fluctuations, females were able to maintain T_{egg} between 34 and 40°C for 82% of the time during the day and between 36 and 40°C for 85% at night (Table 1). The optimum T_{egg} range where thermal factors are most favorable for the incubating female as well as the development of her embryos may lie within this modal range.

Variations in T_{egg} between two eggs in the

same nest tended to be greatest in the daytime, ranging from 0.1 to 4.7°C (Table 2). Observations of behaviors occurring during incubation indicated that small discrepancies were probably due to differences in the contact of eggs with the brood patch. Large differences occurred when the female was off the nest and one egg was exposed to direct sun while the other was shaded. Other workers have measured differences of 4–6°C between central and peripheral eggs in a clutch, especially where clutch size was large (see Huggins 1941).

In view of these intra-clutch differences, we investigated change in egg position in the nest over a 24-h period by noting the location of numbered eggs. Data from seven nests indicated that egg positions changed frequently and randomly. Movement of eggs is important not only for even heat distribution, but also to prevent the developing membranes from growing together, causing mortality or disruption of normal growth (Brody 1945, Romanoff 1960, Robertson 1961).

Eggs constantly experienced rapid temperature changes when females were away foraging. Upon being rewarmed, they were not usually held at a constant temperature for long, but were returned to a "set point" whereupon the female embarked on another foraging trip. The average T_{egg} set point was 38.0°C, SD = 1.5. White and Kinney (1974) suggested that recognition of a critical temperature for ces-

TABLE 2. Mean temperatures per two-hour interval of two eggs (A and B) recorded simultaneously in the same nest for five consecutive days.

Time interval	Egg	Egg temperature, °C			Time interval	Egg	Egg temperature, °C		
		Mean	Min.	Max.			Mean	Min.	Max.
05:30-07:30	A	37.5	32.5	40.2	17:30-19:30	A	37.6	23.9	40.9
	B	37.3	31.9	40.8		B	38.2	22.9	41.5
	ΔT	0.2	0.6	0.6		ΔT	0.6	1.0	0.6
07:30-09:30	A	38.5	31.9	40.9	19:30-21:30	A	38.1	30.9	40.0
	B	37.9	27.0	40.2		B	38.1	31.2	40.9
	ΔT	0.6	4.9	0.7		ΔT	0.0	0.3	0.9
09:30-11:30	A	38.2	32.5	40.2	21:30-23:30	A	38.8	36.0	40.0
	B	38.3	32.4	40.5		B	38.6	35.9	40.5
	ΔT	0.1	0.1	0.3		ΔT	0.2	0.1	0.5
11:30-13:30	A	38.8	37.0	40.1	23:30-01:30	A	38.8	36.0	40.0
	B	38.1	34.2	41.0		B	38.4	36.0	40.9
	ΔT	0.7	2.8	0.9		ΔT	0.4	0.0	0.9
13:30-15:30	A	38.2	25.9	41.3	01:30-03:30	A	38.4	35.8	40.0
	B	37.3	21.2	41.5		B	38.1	36.0	40.2
	ΔT	0.9	4.7	0.2		ΔT	0.3	0.2	0.2
15:30-17:30	A	37.6	27.2	40.9	03:30-05:30	A	38.0	35.8	39.2
	B	38.0	26.6	41.6		B	37.8	35.8	40.1
	ΔT	0.4	0.6	0.7		ΔT	0.2	0.0	0.4

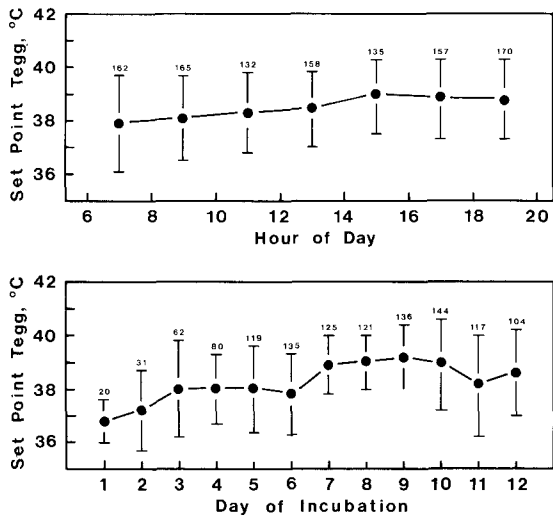


FIGURE 4. Mean set point egg temperatures throughout the active day (upper panel), and throughout incubation (lower panel). Numerals indicate sample size and vertical lines denote standard deviations. Data are from eight nests.

sation of attentiveness is a common phenomenon. In Figure 4, upper, mean set point temperatures based on 1,079 records indicate that it remained remarkably constant during early morning hours when T_a was low (Fig. 2), and throughout the entire day. Examined by day of incubation, however, set point temperature varied slightly, being lower at the onset of incubation than later, and increasing 2°C between Day 1 and Day 4 (Fig. 4, lower). This may be related to brood patch maturation (see beyond).

The small fluctuation in set point temperatures suggests that females must be acutely sensitive to T_{egg} as well as the thermal environment at the nest. In many avian species, the brood patch possesses thermoreceptors (Baerends 1959, Franks 1967, Drent 1970, White and Kinney 1974), and T_{egg} must provide feedback information that is used in governing behaviors that maintain a consistent set point.

Egg temperature changed during periods of constant attentiveness as incubation progressed. Both day and night mean T_{egg} increased during Days 1 to 4 of incubation. From Day 5, onward, mean T_{egg} remained virtually steady (Fig. 5). The initial rise in mean T_{egg} may be due to increased heat transfer abilities by the developing brood patch. Bailey (1952), Farner (1958), Jones (1971), Drent (1975), Afton (1979), and Barrett (1980) found a similar pattern in T_{egg} during early stages of incubation, which they related to brood patch development. Bailey (1952) showed that vascularization of the brood patch in *Z. leucophrys* begins approximately two days before the first

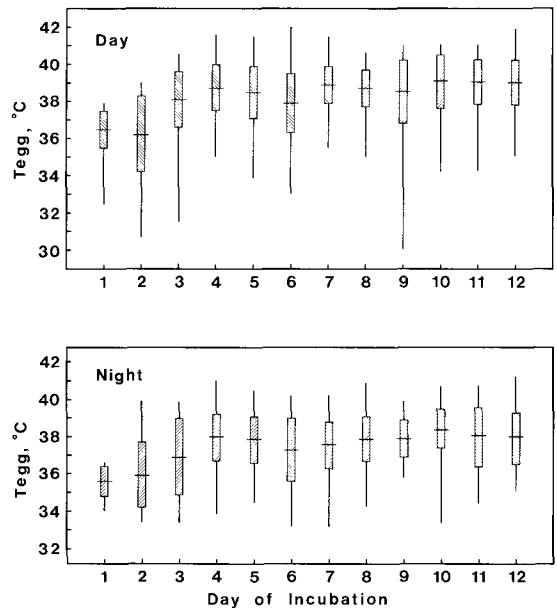


FIGURE 5. Mean egg temperature (horizontal lines) per day of incubation during the day and night. Bars denote standard deviations and vertical lines indicate the range. Temperatures were taken every three minutes during constant attentiveness (after the female had been on the nest for at least 15 min). Total number of measurements from eight nests equals 9,933.

egg is laid and reaches completion on Day 3 or 4 of incubation. Toward the end of this period the dermal tissue begins to swell and thicken and an edematous condition continues throughout the remainder of incubation and during brooding of the young.

T_{egg} was affected not only by T_a when the female left the nest but also by the temperature gradient between egg and ambient environment during constant attentiveness (Fig. 6, upper). There was a slight but highly significant decrease in T_{egg} with fall in T_a ($r = 0.31$, $P < 0.001$). A similar relationship has been found in other species (Von Haartman 1957, Ken-deigh 1963, Mertens 1977b, 1980, Haftorn 1978, 1979).

Although mean T_{egg} in *Z. l. oriantha* declined slightly as the external environment cooled, a high thermal gradient from the nest to the environment was maintained. Incubating females usually were able to maintain T_{egg} within an optimal range (34–38°C) even during the coldest nights. Variations in T_{egg} that occurred within this range mainly occurred in eggs in aerial nests. T_{egg} in ground nests remained relatively stable, especially between 4 and 25°C T_a and were generally higher than those in aerial nests (Fig. 6, lower). Low T_a s seemed to be more critical for eggs in nests situated above ground, probably because heat was lost more rapidly by convective cooling.

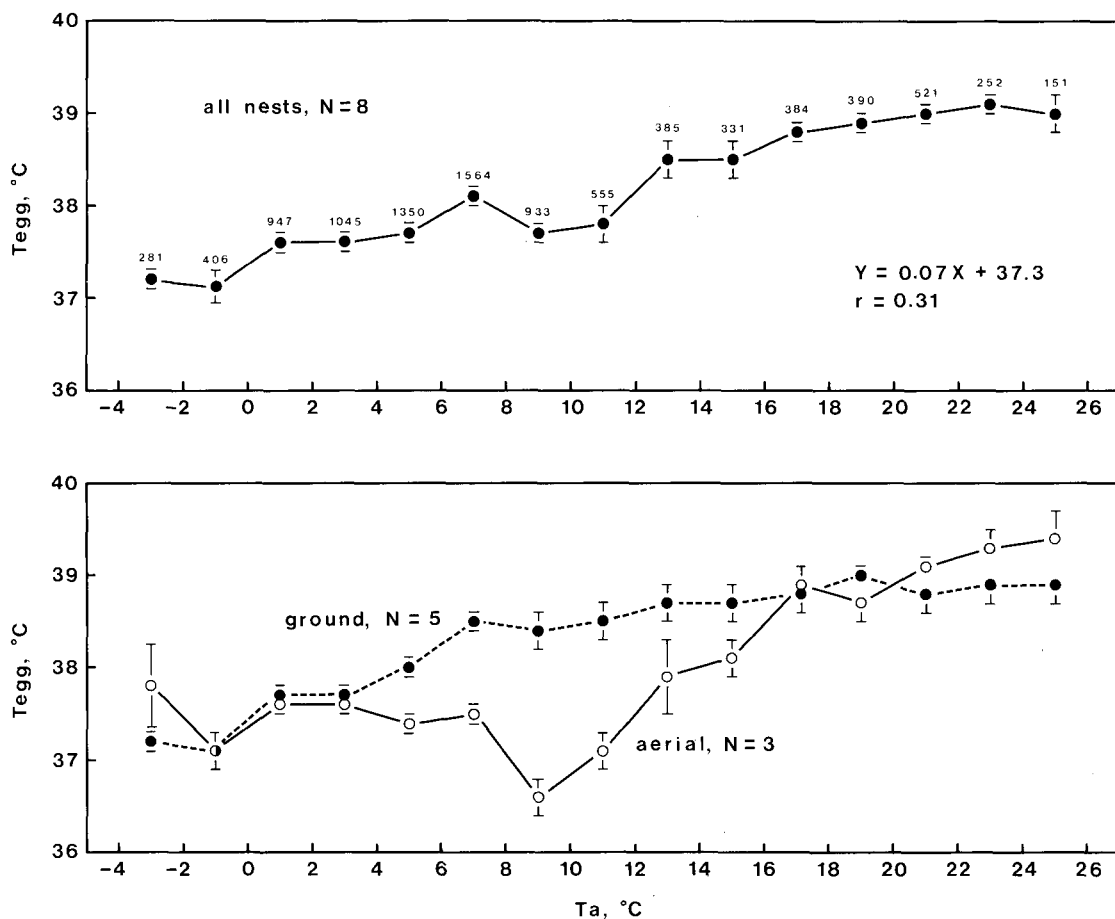


FIGURE 6. Mean egg temperature vs. air temperature measured every three minutes during constant attentiveness (after female had been on the nest for at least 15 min) for all nests (upper panel) and separated by nest location (lower panel). Numerals in upper panel give sample size. Two standard errors of mean shown in all cases.

This was particularly evident at T_a s between 8 and 16°C where T_{egg} in aerial nests began to decrease markedly (Fig. 6, lower). At T_a s below 8°C however, mean T_{egg} increased, probably because the females produced more heat.

An analysis of all our records shows that mean T_{egg} was significantly higher in ground than in aerial nests (37.5°C vs. 36.8°C, $P < 0.01$). The absolute difference here was not great, however, and did not seem to affect hatchability; 140 ground nests (540 eggs) showed 95% hatchability, and 109 aerial nests (421 eggs) showed 91% hatchability. Nests included in this analysis were found between 1968 and 1980 and were not manipulated by investigative techniques other than direct observations.

Adjustments in heat production by females using aerial nests are apparently in subtle, small increments because recordings at T_a s below 8°C do not show marked upswings in T_{egg} at any time. T_{egg} in ground nests tended downward with decreasing T_a through the range of T_a s depicted (Fig. 6, lower) but always exceeded

37°C. On one exceptional night, however, T_a fell to -7.8°C when we were recording from a ground nest. In this instance, T_{egg} declined steadily during the early morning (Fig. 7). At about 04:00 T_{egg} was at a low of 33.5°C, it then began to increase and during the next hour reached 38.0°C. The female on these eggs was presumably engaged in shivering thermogenesis a good deal of the time between 04:00 and 06:00. At about 06:00 she made her first foraging trip of the day and T_{egg} was affected thereafter in the usual way.

Nests seem to provide such a favorable microclimate for the incubating female that she may not have to raise her metabolic rate except on the coldest of nights. This fits with previous information that female *Z. l. oriantha* maintain modest fat stores and are in positive energy balance throughout incubation (Morton 1976, 1977) and with the findings that these sparrows realize energy savings of about 15% during incubation due to ameliorating effects of the nest (Walsberg and King 1978a). In the Zebra Finch (*Poephila guttata*) the ameliorat-

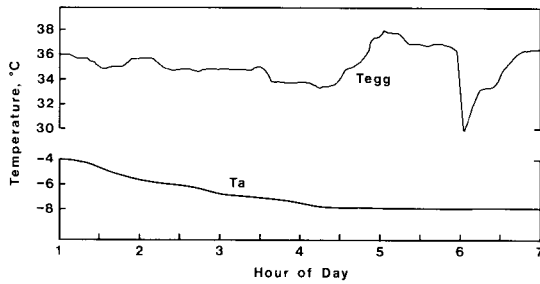


FIGURE 7. Egg temperature (T_{egg}) in a ground nest during a period of unusually low air temperature (T_a).

ing effects of the nest microclimate approximately compensate for the energetic cost of incubation (Vleck 1981). Likewise in Starlings (*Sturnus vulgaris*), heat from normal metabolism is sufficient to maintain T_{egg} even at subfreezing ambient temperatures (Biebach 1979).

T_{egg} data suggest that ground nests were more favorable energetically to incubating females than aerial nests and, other factors being equal, should be the location of choice. We found indications that this is true (Table 3): 57% of the 552 nests discovered thus far in which at least one egg was laid were built on the ground ($\chi^2 = 10.5$, $P < 0.01$). In this analysis, all nests and re-nests of color-banded breeding pairs were located from 1978 to 1981. Techniques for finding nests were consistent from 1968 to 1981, so the likelihood of sighting ground and aerial nests was relatively equal from year to year.

Other factors, such as weather and predation, may affect *Z. l. oriantha* nests differentially, depending upon nest location (see Morton et al. 1972), but the time when the habitat becomes available for nesting each season seems to be of major importance. Habitat availability is most simply measured by the snowpack; the deeper the pack, the later suitable nesting sites are available. In heavy snow years the ground is sodden, covered with running water, and devoid of thick grass cover until quite late. Under these circumstances nesting is delayed somewhat but eventually proceeds, a large share of nests being built in willows and pines (Morton 1978). Later in the season as ground cover increases, nests are built on the ground. In light snow years, ground cover is adequate at the time birds are first ready to nest and most nests are built on the ground. Nest location is clearly related to snow depth (i.e., habitat availability; $r = -0.89$, $P < 0.01$; Fig. 8).

NEST ORIENTATION

Birds of many species have been found to orient their nests in relation to environmental

TABLE 3. Annual location of nests and snow depth measured at the study area ca. 1 April (State of California Snow Survey).

	Number of nests				Snow depth, cm
	Ground	(%)	Aerial	(%)	
1968	24	(59)	17	(41)	113
1969	12	(22)	43	(78)	342
1970	45	(61)	29	(39)	176
1973	13	(46)	15	(54)	204
1976	58	(87)	9	(13)	79
1978	29	(49)	30	(51)	263
1979	49	(57)	37	(43)	227
1980	38	(46)	44	(54)	264
1981	46	(77)	14	(23)	160
Totals	314	(57)	238	(43)	

variables. In some species in some habitats nest orientation is known to be nonrandom, apparently in order to avoid solar radiation or to use it as a heat source (Dorst 1962, 1963, Hadley 1969, Maclean 1970, Orr 1970, Riehm 1970, Dawson 1976, Inouye 1976). Other species situate their nests away from prevailing winds (Ricklefs and Hainsworth 1969, Conner 1975, Schaefer 1980). Factors affecting nest orientation may therefore be primarily related to thermal environments (Calder 1971, 1973, 1974, Balda and Bateman 1973, Austin 1974, 1976, Southwick and Gates 1975, Carpenter 1976, Southwick 1977, Inouye et al. 1981, Walsberg 1981). Nest orientation furthermore may be important to the maintenance of "normal" incubation temperatures as well as the body temperature of the incubating female.

At Tioga Pass female White-crowned Sparrows seemed to select sites for their nests that were nonrandom with respect to the surrounding vegetation (Rayleigh Test, $r = 0.48$, $P < 0.01$). Measurements of 106 nest placements indicated that northeastern sides of bushes were preferred (Fig. 9). This type of orientation may be protective because prevailing winds, especially the cold winds of early morning, and storms come from the south at Tioga Pass during the nesting season. In the daily weather log kept at Tioga Pass for the past 10 years by the U.S. Park Service, 74% of winds noted were from the south during June and July. Brisk winds are common here and, coupled with low T_a s, could be a potent thermolytic agent. This would seem especially true for embryos in aerial nests since they are more likely to lose heat by convective cooling (Fig. 6, lower) and to be damaged by storms (Morton et al. 1972). Another advantage of nest placement on the northeastern side of cover may be to ensure shading and to ameliorate heat stress during midday. Exposure of the nest interior to direct sun averaged only 58% at midday. Walsberg

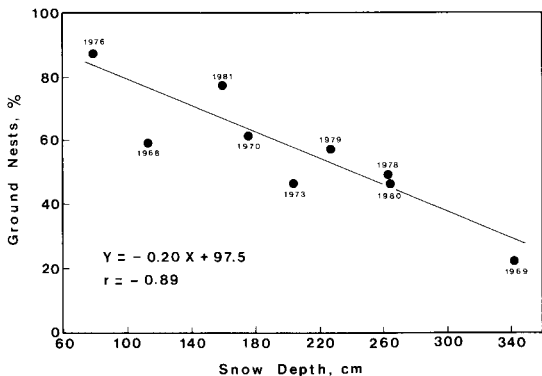


FIGURE 8. Relationship of snow depth (habitat availability) to nest location at Tioga Pass.

and King (1978a) found that nest placement of *Z. l. oriantha* in Oregon did not show a particular orientation but that nest canopies did; exposure tended to be greatest toward the east, therefore nests were heated by solar radiation in the morning and shaded in the afternoon. Verbeek (1981) showed that Water Pipit (*Anthus spinoletta*) nests tend to be oriented toward the northwest or northeast, but these nests were not more successful than those oriented otherwise. He suggested that nests are oriented not for egg protection, but to prevent possible discomfort and harm to the incubating female. Additional studies are needed to elucidate the effects of wind, solar radiation and other weather conditions on nest site selection.

SUMMARY AND CONCLUSIONS

Female *Z. l. oriantha* hatch their eggs in an environment where T_a is usually near freezing at night, brisk cold winds and storms are common, and solar radiation can be intense. Despite wide variations in ambient conditions, eggs were maintained between 34 and 40°C for 82% of the day and between 36 and 40°C for 85% of the night. Overall mean T_{egg} for the whole incubation period was 37.3°C, SD = 2.3.

T_{egg} varied considerably throughout the day. Embryos were able to tolerate low and oscillating temperatures during their development. This allowed the female to forage in the cold hours of early morning and late afternoon. During exposure to direct sun however, females sometimes truncated their foraging, staying on the nest to prevent embryos from being overheated.

Temperatures differed between eggs in a clutch and differences tended to be greater in the daytime than at night. Since egg position was changed frequently and randomly, heat was probably distributed evenly to all eggs.

Eggs constantly experienced rapid changes in temperature when females were foraging.

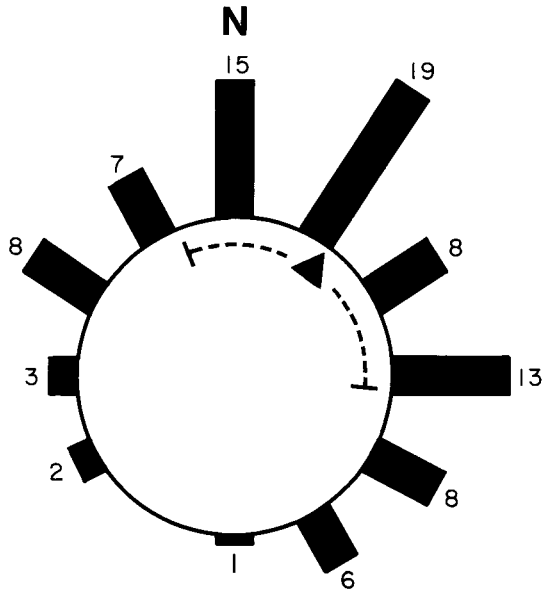


FIGURE 9. Orientation of 90 nests at Tioga Pass. The number of nests in specific compass directions is indicated by the length of the bars and the numeral at the end of each bar. Only nests placed at the edge of cover are shown. An additional 16 nests (not represented) were located centrally. The triangle indicates mean direction of orientation. Dispersion about the mean direction, the angular deviation, is indicated by the dashed line (see Batschelet 1965).

Upon being rewarmed they were not usually held at a constant temperature for an extended period, but were returned to a set point, whereupon the female departed for more foraging. Set point temperatures were remarkably constant throughout the day, suggesting that females must be acutely sensitive to T_{egg} as well as the thermal environment at the nest. T_{egg} must provide information that is used in governing behaviors that result in attainment of optimum egg temperatures.

Mean egg temperature changed during periods of constant attentiveness (15 min or longer) as incubation progressed. Both day and night mean T_{egg} increased during early stages of incubation. This initial rise in mean T_{egg} was probably due to increased heat transfer abilities of the developing brood patch.

T_{egg} was affected by the temperature gradient between egg and environment during constant attentiveness. Mean T_{egg} declined slightly as the external environment cooled, but incubating females were usually able to maintain T_{egg} within an optimal range (34–38°C) even during cold nights. The nest may provide such a favorable microclimate for the incubating female that she may not have to increase metabolic rate to maintain her body temperature except at very low T_a s.

Overall mean T_{egg} was significantly higher in ground than in aerial nests. The absolute dif-

ference was not great, however, and did not seem to affect hatchability. Eggs in aerial nests were probably cooler than those in ground nests at similar ambient temperatures because heat was lost more readily from them by convective cooling. Hence, a female's energetic cost of incubation may be greater in aerial nests and therefore ground nests should be favored. However, other factors such as weather, predation, and habitat availability, also affect selection of nest location. Of these, at Tioga Pass the time at which the habitat becomes available is probably most important in affecting selection for nest height.

Orientation of nests with respect to the vegetational mass in which they are built may be important to the maintenance of normal incubation temperatures. Females selected sites for their nests that were nonrandom with respect to surrounding vegetation, preferring northeastern sides of bushes. Such orientation may be protective because prevailing winds, especially the cold winds of early morning, and storms usually come from the south at Tioga Pass during the nesting season. Another advantage of nest placement on the northeastern side of cover may be to enhance shading, thus decreasing heat stress during midday.

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