

INCUBATION TEMPERATURES OF WILSON'S PLOVERS AND KILLDEERS¹

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Abstract. Internal egg temperatures (T_e), nest bottom temperatures (T_n), and shaded air temperatures (T_a) were measured in Wilson's Plover (*Charadrius wilsonia*) nests near the Texas coast, and at a Killdeer (*C. vociferus*) nest in Virginia. During daylight incubation, T_e in Wilson's Plovers was $36.2 \pm 1.3^\circ\text{C}$ (mean \pm SD, range = 31.0 – 39.7°C), and T_e in Killdeers was $35.2 \pm 2.3^\circ\text{C}$ (range 29.2 – 42.5°C). Mean T_n values during daylight incubation were lower ($33.5 \pm 4.0^\circ\text{C}$, and $23.6 \pm 6.0^\circ\text{C}$, respectively). The maximum T_e in eggs that hatched was 39.9°C in Wilson's Plovers and 42.8°C in Killdeers. Linear regressions of T_e and T_n on T_a during daylight incubation were significant in both species, with slopes ranging from 0.32 to $0.88^\circ\text{C}/^\circ\text{C}$. Partial correlations (third- or fourth-order) of T_e with T_e and T_n for daylight data were significant in all cases (range = 0.63 – 0.85). In some data sets, variables for nest substrate (soil or pavement), parental behavior (on or off the nest), day of incubation, and hour of the day also had significant partial correlations with T_e or T_n . Cooling and warming rates of uncovered eggs in nests ($^\circ\text{C}$ change in T_e /min) varied inversely with ($T_e - T_a$) in both species, and hourly cooling rates were $4.4^\circ\text{C}/^\circ\text{C}\cdot\text{hr}$ in Wilson's Plovers, and $5.9^\circ\text{C}/^\circ\text{C}\cdot\text{hr}$ in Killdeers, both higher than rates predicted for eggs in an environmental chamber. Behavioral regulation of T_e was achieved by varying attentiveness, shading the eggs, sitting on the eggs when T_e was over 38°C , or belly soaking. Four pairs of Wilson's Plovers nesting on pavement used belly soaking 24 times during 750 hr of observation, when T_n was $41.8 \pm 1.6^\circ\text{C}$ (Range = 38.9°C – 44.2°C). Belly soaking appeared to be rare because nests on soil were not hot enough to require it, and because most nests were far from water.

Key words: Incubation; egg temperature; nest-bottom temperature; egg-cooling rate; Wilson's Plover; *Charadrius wilsonia*; Killdeer; *Charadrius vociferus*.

INTRODUCTION

Incubation can be defined as the application of heat to eggs (Beer 1964, White and Kinney 1974). However, this definition is incomplete, since in many climates eggs must be cooled as well as heated. Avian embryos are more quickly killed by overheating than by chilling (Bennett and Dawson 1979). Any bird nesting where shaded air temperature (T_a) reaches about 40°C , or where strong sunlight hits the eggs at lower T_a (Bennett et al. 1981), may need to cool its eggs. Thus, a more general definition of incubation is the "regulation . . . of physical factors influencing development" (Drent 1975).

Shorebirds, especially Charadrii (plovers and allies), sometimes nest in hot climates where T_a reaches 45°C . They cool their eggs by a combination of three methods: shading, constant tight sitting, and belly soaking (Grant 1982). Most studies of incubation temperatures of shorebirds

nesting in hot climates have been done in habitats where belly soaking was used frequently at most or all nests (Purdue 1976, Howell 1979, Grant 1982). While this is an effective method of egg cooling, it requires nesting near water and frequent trips to get water by the parents, so that it may not be feasible in all nesting habitats in hot climates.

I studied two species of plovers nesting in hot climates (maximum $T_a = 36^\circ\text{C}$ – 45°C) that did not use belly soaking, or used it rarely. I measured incubation temperatures (internal egg temperature [T_e] and nest bottom temperature [T_n]), T_a , and parental behavior at 13 nests of Wilson's Plovers (*Charadrius wilsonia*) on the Texas coast. For comparative purposes, I collected the same data at a Killdeer (*C. vociferus*) nest in western Virginia. Killdeer eggs are only slightly larger than Wilson's Plover eggs. The data show how effective shading and sitting were at regulating T_e and T_n , without using belly soaking in most cases. They also show the environmental conditions under which each behavior was used, including the few occurrences of belly soaking in Wilson's Plover.

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MATERIALS AND METHODS

I studied Wilson's Plovers at Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas (Bergstrom 1988). I recorded T_n and T_a continuously for a total of 39 days at 11 nests in 1980, between 3 May and 24 June. Six of these nests were on soil, and five were on asphalt or concrete pavement. In 1981 I recorded T_e , T_n , and T_a and observed parental behavior at two nests at Matagorda Island, one on soil and one on pavement, for a total of 15 hr (during daylight only) on 29 and 30 May. I studied a Killdeer nest in Rockbridge County, Virginia, 3.4 km northeast of the city of Lexington. I recorded T_e , T_n , and T_a continuously at this nest for 14 days between 12 and 25 May 1988. The nest was located at the edge of a driveway surfaced in dark crushed limestone, on an exposed hilltop at an elevation of 349 m.

Temperatures were measured with thermistors in 1980 and 1981, and with thermocouples in 1988. In 1980, I used two Atkins telethermometers and a Rustrak two-channel chart recorder. T_n was measured in the bottom of the nest cup with a flat thermistor 2.1 mm thick, and T_a was measured in the partial shade of vegetation near the nest, 5 cm off the ground, with a cylindrical stainless steel probe 3.3 mm in diameter. Temperatures from the strip chart records were digitized to the nearest 0.1°C every 15 min. In 1981, temperatures were measured with a YSI telethermometer, with a YSI 424 probe glued with the tip in the center of the egg, a YSI 423 probe in the bottom of the nest cup, and a YSI 408 probe in the partial shade of vegetation 5 cm off the ground near the nest (YSI, Yellow Springs, Ohio). Measurements were recorded whenever parental behavior changed, or when T_e changed by 0.5°C or more. In 1988, temperatures were measured with 30-gauge copper-constantan thermocouples, and recorded to the nearest 0.1°C with an ADC-1 interface (RMS, Seattle, Washington) and a PC-8201 microcomputer (NEC Home Electronics, Elk Grove, Illinois) every 5 min. T_e was recorded in the air cell of an egg that hatched with the other eggs, touching the inner membrane, T_n was measured at the bottom of the nest cup, and T_a was measured with a thermocouple dipped in white paint, placed in the partial shade of vegetation 5 cm above the ground, 60 cm from the nest on the same crushed rock driveway. In all cases, the temperature-measur-

ing apparatus was calibrated against an accurate (to 0.1°C) mercury thermometer, over the range of temperatures encountered in the field, before and after each use.

Parental behavior was determined visually along with T_e and T_n during the day, because T_e did not always fall during absences. For Wilson's Plovers in 1980, Super 8 movie cameras filmed the nest at 1-min intervals throughout the daylight hours. In 1981, parental behavior was observed directly from a blind. Daytime attentiveness in Killdeers was determined by changes in the output of a silicon solar cell placed under the eggs. Parental behavior at the nest was classified in five categories: tight sit (eggs not visible), shading (eggs visible, includes "loose sit" [Grant 1982]), off the nest (daylight), and on or off the nest at night. Mean T_e and T_n were calculated for data from daylight tight sitting only, and for all data. Linear regressions of T_e and T_n on T_a were calculated only with data from daylight tight sitting, for comparison to other studies and to assess the degree of regulation of T_e when a parent was on the eggs and T_a was high. Partial correlations were calculated from daylight data during all behaviors, to facilitate comparisons among data sets; no night data were collected in 1981.

Attentiveness was calculated as the percentage of each daylight hour that the nest was covered by a parent, either in tight sitting or shading. Shading time was corrected for differing amounts of attentiveness, by multiplying the % of the hour spent shading by the attentiveness for each parent, and then dividing the sum of both parents' values by the total attentiveness for that hour. Thus, if total attentiveness was 60% and all of it was shading, shading time would be 100% for that hour.

Statistical analyses were done with SPSS-X (SPSS 1983) and Minitab (Minitab 1986). Deviations from normality were checked for all data sets, and if they were significant ($P < 0.05$), either nonparametric tests or transformations were used. Because the distributions of incubation temperatures, especially T_e measured during all behaviors, were sometimes skewed left (because cooling is more common than heating) and peaked or leptokurtic (because they are regulated), a probit transformation (Sokal and Rohlf 1987) was required in some cases to achieve normality. Descriptive statistics given are mean \pm standard deviation.

TABLE 1. Descriptive statistics for internal egg temperature (T_e), nest bottom temperature (T_n), and shaded air temperature (T_a) in Wilson's Plover and Killdeer.^a

	Wilson's Plover		Killdeer
	1980	1981	
T_e			
All data	—	36.4 ± 1.3 (31.0–39.9, 329)	33.7 ± 3.4 (16.0–42.8, 3,662)
Day incubation ^b	—	36.2 ± 1.3 (31.0–39.7, 160)	35.2 ± 2.3 (29.2–42.5, 1,602)
T_n			
All data	33.5 ± 4.2 (22.7–48.5, 2,419)	34.2 ± 1.5 (30.3–37.5, 326)	23.5 ± 6.1 (12.6–38.2, 2,389)
Day incubation	33.5 ± 4.0 (24.7–44.0, 865)	33.8 ± 1.4 (30.3–37.5, 158)	23.6 ± 6.0 (12.6–37.4, 1,256)
T_a			
All data	29.9 ± 5.2 (16.4–45.3, 2,419)	33.3 ± 2.3 (27.2–39.0, 226)	20.1 ± 6.0 (9.8–36.5, 3,662)
Day incubation	30.3 ± 4.9 (16.4–45.3, 856)	32.9 ± 2.4 (27.8–37.2, 109)	21.5 ± 5.5 (9.8–35.4, 1,602)

^a $\bar{x} \pm SD$ (min–max, n).

^b A parent was sitting tightly on the eggs.

Because several of the other variables that could affect incubation temperatures are correlated with T_a and with each other, partial correlation was used to assess the unique effect of each variable (SPSS 1983). For this analysis, dummy variables, coded 0 or 1, were created to assess the effects of nest substrate (soil or pavement) and parental behavior (on or off the nest) on incubation temperatures. A conservative P level was used (two-tailed $P < 0.002$) because 21 correlations were calculated. Analysis of covariance (SPSS 1983) was used to compare the slopes of regression lines of T_e and T_n on T_a at Wilson's Plover nests on soil and pavement.

RESULTS AND DISCUSSION

MEAN INCUBATION TEMPERATURES

Mean T_e and T_n were higher in Wilson's Plover nests than in the Killdeer nest (Table 1), but this was probably due to the dependence of T_e and T_n on T_a , and the lower T_a values at the Killdeer nest (see below). In both Wilson's Plovers and Killdeers, T_e was significantly higher than T_n (Table 1; Wilcoxon's matched-pairs test, $P < 0.0001$ in both species). In Wilson's Plovers in 1981, T_n was significantly higher at the nest on pavement than at the nest on soil (medians 34.8°C vs. 34.0°C, Mann-Whitney $z = 6.6$, $P < 0.0001$), but neither T_e nor T_a differed significantly between the two nests ($P = 0.15$ and 0.56). The two nests

were observed for similar daylight periods on consecutive days with similar weather. I made other statistical comparisons using partial correlation (see below) to control for the effects of variation in T_a and other variables.

Mean T_e values during incubation in these plovers are similar to those reported for other charadriiforms (Drent 1975, p. 338), in spite of the hot climates in Texas and Virginia. The T_n values are lower than those reported for other charadriiforms (Drent 1975, p. 354), probably because T_n is usually measured above the nest floor.

UPPER LIMITS OF T_e AND T_n

In embryonic Heermann's Gull's (*Larus heermanni*), the heart stopped when T_e reached 40–41°C, and the embryo died when kept at 43°C for 1 hr (Bennett and Dawson 1979). Embryonic Western Gulls (*L. occidentalis*) had a heartbeat up to 46°C and died at 47–49°C, however (Bennett et al. 1981), and a Black-necked Stilt (*Himantopus mexicanus*) embryo survived temperatures up to 46°C (Grant 1982). Similar data are not available for plovers.

In Wilson's Plovers, T_e reached a maximum of 39.9°C, when T_n was 37.5°C. This temperature was maintained for only 1 min during an absence. The measurements of T_e were only made for 2 days, which did not include the hottest days

during the breeding season. During longer measurements of T_n over 39 days in 1980, including some of the hottest days of the season, a maximum of 48.5°C was reached once, but it was unlikely that the eggs were that hot; the probe was under the eggs on pavement, which was probably hotter than the air. Using a linear regression of T_e on T_n from the 1981 data, I estimated that $T_e = 42^\circ\text{C}$ (chosen as the start of overheating) would be reached when $T_n = 43.2^\circ\text{C}$. T_n exceeded 43.2°C in 12 of the 1,637 daylight measurements in 1980 (0.7%), all between 12:00 and 16:00, and all in pavement nests. Belly soaking was used in three of those cases (see below). Five eggs failed to hatch in 1980 out of 39 eggs that survived to hatching, but the causes of failure are unknown. Two of the five eggs were on a cooler soil substrate, so overheating was probably not the only cause of their failure to hatch.

In the Killdeer nest, maximum T_e was 42.8°C, during an absence, and T_e exceeded 42°C five times in 2,269 daylight measurements (0.2%). Since none of those were consecutive, and all four eggs hatched, embryos apparently can withstand such temperatures for up to about 5 min. When the parents were shading the eggs, the maximum T_e was 41.2°C.

T_e in Killdeers at the Salton Sea reached 41.7°C, and exceeded 41°C in four of 142 daylight measurements. Belly soaking was frequent there (Grant 1982, p. 38). Measurements were not made during absences, however. Snowy Plover (*C. alexandrinus*) eggs in Oklahoma reached maxima of 42–43°C in four of 775 daylight measurements (including absences), probably also moderated by belly soaking (Purdue 1976).

EFFECTS OF T_a AND OTHER VARIABLES ON T_e AND T_n

Linear regressions of T_e and T_n on T_a during daytime incubation were significant in both species, with slopes between 0.32 and 0.88 (Fig. 1). Similar regressions of T_e on T_a in Killdeers were found by Grant (1982) at the Salton Sea and by Cronan (1974) in Oregon. Purdue (1976) found a higher slope of T_e on T_a , 0.63, for Snowy Plovers in Oklahoma, but he measured T_e during absences as well as incubation, and used an unshaded thermistor for T_a .

In Wilson's Plovers, the regressions of T_e and T_n on T_a during daylight incubation had significantly lower slopes at nests on soil than at nests on pavement. In 1980, the slopes of T_n on T_a

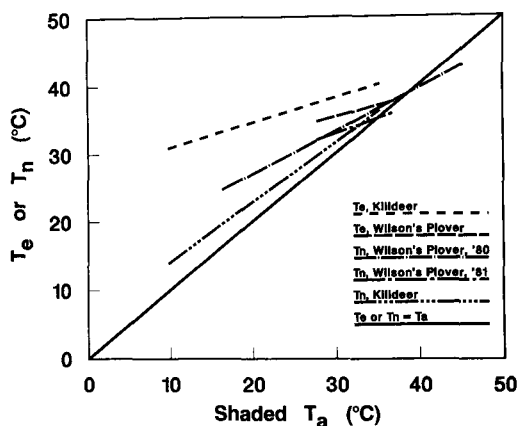


FIGURE 1. Linear regressions of T_e and T_n on T_a for data from day incubation in Wilson's Plovers and Killdeers. Equations for Wilson's Plovers were $T_e = 25.7 + 0.32 T_a$, $R^2 = 43\%$, $n = 109$; $T_n = 14.5 + 0.63 T_a$, $R^2 = 59\%$, $n = 856$ (1980); $T_n = 20.1 + 0.43 T_a$, $R^2 = 60\%$, $n = 104$ (1981). Equations for Killdeers were: $T_e = 27.3 + 0.36 T_a$, $R^2 = 72\%$, $n = 1,602$; $T_n = 5.32 + 0.88 T_a$, $R^2 = 59\%$, $n = 1,256$. All regressions were significant ($P < 0.001$).

were 0.49 on soil and 0.67 on pavement ($F = 123.2$, $df = 1$, 852, $P < 0.0001$). In 1981, the slopes of T_n on T_a were 0.28 and 0.51, respectively ($F = 11.5$, $df = 1$, 104, $P = 0.001$), and the slopes of T_e on T_a were 0.23 and 0.53, respectively ($F = 20.9$, $df = 1$, 105, $P < 0.0001$). Pavement nests probably had higher slopes because they were unlined, exposing the eggs to greater heat fluxes with the substrate. Cronan (1974) found a slope of T_e on T_a of 0.17 at a Killdeer nest fully lined with wood chips, compared to slopes up to 0.34 at nests with less lining.

Third- or fourth-order partial correlations of T_e and T_n with T_a , controlling for three or four other variables, were also significant and positive for all daylight data in both species (Table 2). There was a significant positive correlation between nest substrate (soil or pavement) and T_n in Wilson's Plovers in both years, showing higher T_n on the pavement, probably due to greater heat conduction in the unlined pavement nests (see above). A similar significant correlation with T_e was probably absent because T_n was measured closer to the substrate. A significant negative correlation was found between parental behavior (on or off the nest) and T_e in Killdeers, showing cooling during absences, and the positive correlation with T_n in Wilson's Plovers shows slight warming during absences.

TABLE 2. Partial correlations (third- or fourth-order) between T_e or T_n and T_a and other variables for daylight data in Wilson's Plovers and Killdeers.

Species	Year	Variable	Partial correlations with:					df
			T_e	Soilpav	Onoff	Dayinc	Hour	
WP	81	T_e	0.63	(-0.12)	(-0.12)	—	(-0.01)	221
KL	88	T_e	0.74	—	-0.52	0.11	(-0.05)	2,252
WP	81	T_n	0.77	0.32	(0.11)	—	0.36	221
WP	80	T_n	0.78	0.36	0.08	-0.09	0.50	1,584
KL	88	T_n	0.85	—	(-0.02)	0.54	-0.10	1,690

Notes: WP = Wilson's Plover, KL = Killdeer, Soilpav = soil vs. pavement nests, Onoff = bird on vs. off the nest, Dayinc = day of the incubation period (1-25), — = no data available. All correlations were significant (two-tailed $P < 0.002$) except those in parentheses.

Day of the incubation period had positive correlations with T_e and T_n in Killdeers, showing warming toward hatching, but its correlation with T_n in Wilson's Plovers was negative, although small. Both temperatures rose toward hatching in Herring Gulls (*Larus argentatus*, Drent 1970). The day of incubation data are more meaningful in Killdeers, because each Wilson's Plover nest was observed for only 3-6 days. Hour (using a range of 6-20 hr) had positive correlations with T_n in both data sets for Wilson's Plovers, but had a negative correlation with T_n in Killdeers. These correlations could be caused by diurnal changes in parental behavior (Haftorn 1981), or by diurnal changes in environmental factors (such as rising soil temperature) not correlated with T_a .

COOLING AND WARMING RATES OF UNCOVERED EGGS

Uncovered eggs should cool or warm at a rate proportional to the difference between T_e and T_a , according to Newton's law of cooling. The cooling rate is calculated from the slope of a regression of the rate of change in T_e on $(T_e - T_a)$, and it represents the predicted $^{\circ}\text{C}$ drop in T_e per $^{\circ}\text{C}$ difference between T_e and T_a per hour, abbreviated as $^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$ (Drent 1970). In an environmental chamber, the predicted cooling rate for Wilson's Plover eggs (weighing about 12 g) is $2.4^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$, and would be slightly lower for Killdeer eggs weighing about 14 g (Drent 1975). Rates for uncovered eggs in a nest may be higher than this, due to conductive and convective heat losses (Drent 1975), or they may be lower in well-insulated waterfowl nests (Afton 1979).

The rates of change in T_e ($^{\circ}\text{C}/\text{min}$) of Wilson's Plover and Killdeer eggs in nests were negatively correlated with $(T_e - T_a)$ during daytime absences (Fig. 2). The slopes of the regression lines correspond to standard hourly cooling rates of $4.4^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$ for Wilson's Plovers, and $5.9^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$ for Killdeers, although cooling is a misnomer since warming also occurred. Both rates are higher than the predicted values, and the larger Killdeer egg did not have the predicted lower rate.

Afton (1979) found lower than predicted cooling rates for Northern Shoveler (*Anas clypeata*) eggs, 0.22 rather than $1.1^{\circ}\text{C}/^{\circ}\text{C}\cdot\text{hr}$. He attributed this to the greater insulation in the shoveler nest compared to the exposed egg used for the predicted value. The higher than predicted rates of egg cooling in both plovers show that they have poor nest insulation, and that conductive and convective fluxes probably affect their egg-cooling and warming rates.

BEHAVIORAL REGULATION OF T_e

Behavioral regulation of T_e was accomplished four ways: varying attentiveness with T_a , shading the eggs, sitting on the eggs, and belly soaking, except belly soaking was not seen in Killdeers. Attentiveness varied strongly with T_a in both species, with a U-shaped relationship that was fit by quadratic regression (Bergstrom 1982). In Wilson's Plovers, predicted attentiveness (calculated over 3.5-hr periods) fell from 92% at $T_a = 24.0^{\circ}\text{C}$ to a minimum of 68% at 30.5°C , and then rose to 100% at 41.0°C (Bergstrom 1982). In Killdeers, predicted attentiveness fell from 99% at 12.8°C to a minimum of 76% at 26.3°C , then rose to 87% at 35.3°C .

Variation of attentiveness with T_a occurs in many birds (White and Kinney 1974, Drent 1975). A continuous decrease of attentiveness with increasing T_a is fairly common, and it has been used to support the argument that the main function of incubation is to apply heat to the eggs (White and Kinney 1974). However, a decrease in attentiveness with rising T_a followed by an increase in attentiveness at high T_a occurs in several birds nesting in hot climates (Jayakar and Spurway 1965; MacLean 1967, 1976; Purdue

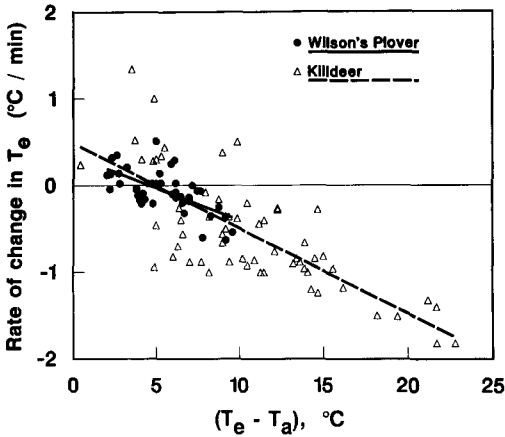


FIGURE 2. Egg cooling and warming rates per minute vs. $(T_e - T_a)$ of uncovered Wilson's Plover eggs in Texas (42 absences) and a Killdeer egg in Virginia (60 absences), all during daylight. Linear regression equations were: Wilson's Plover rate = $0.34 - 0.073 (T_e - T_a)$, $R^2 = 41\%$; Killdeer rate = $0.49 - 0.098 (T_e - T_a)$, $R^2 = 56\%$. Both regressions were significant ($P < 0.0001$).

1976; Yom-Tov et al. 1978; Grant 1982). This suggests that incubation is used to regulate T_e , involving either heating or cooling the eggs depending on conditions (Jayakar and Spurway 1965). Factors affecting attentiveness and other incubation behaviors in these plovers will be analyzed in more detail in a future paper.

T_e always exceeded T_a in Wilson's Plovers, except for two measurements at the nest on pavement. When $T_e > T_a$, the parent can usually cool the eggs by shading them, since T_e will approximate T_a during shading (Carey 1980). Shading the eggs began in Wilson's Plovers when $T_a > 23^\circ\text{C}$ and in Killdeers when $T_a > 25^\circ\text{C}$. Above these temperatures, Wilson's Plovers spent $27.6 \pm 32.5\%$ ($n = 614$) of their time and Killdeers

spent $28.1 \pm 28.6\%$ ($n = 70$) of their time on the nest shading, with the rest of their time on the nest spent sitting. At the Salton Sea, Killdeers spent 60.4% of their time on the nest shading (including loose sit) when $T_a > 31.5^\circ\text{C}$, and Snowy Plovers spent 78.4% of their time shading when $T_a > 29.0^\circ\text{C}$ (Grant 1982), but some of that time was spent belly soaking in both species.

Whether shading or sitting was used to cool the eggs depended on T_e in Wilson's Plovers (Table 3). At the two Wilson's Plover nests I studied in 1981, I observed 15 cases when the eggs cooled for three or more consecutive readings while a parent was on the nest. The parent used sitting to cool the eggs three out of three times when $T_e > 38^\circ\text{C}$, and it used shading 10 out of 12 times when $T_e < 38^\circ\text{C}$. T_a appeared to have a less direct effect on incubation posture than T_e did (Davis et al. 1984): T_a exceeded 35.9°C in eight of the 15 cases of cooling; sitting was used three times, and shading the other five times. T_a was only 36.0°C during two of the three times sitting was used.

Shading the eggs during warm weather occurs in many other birds (Drent 1970). Most of the shorebirds nesting at the Salton Sea use it, except the long-legged Black-necked Stilts and American Avocets, *Recurvirostra americana* (Grant 1982). Tight sitting is less common as a means of egg cooling in shorebirds. Double-banded Coursers (*Rhinoptilus africanus*) switched from shading to tight sitting as T_a exceeded 36°C (MacLean 1967). This desert-nesting species did not use belly soaking. Constant tight sitting is the main behavior used to regulate T_e in desert-nesting doves (Walsberg and Voss-Roberts 1983).

Belly soaking was not seen at the Killdeer nest, and it was uncommon at Wilson's Plover nests. I detected it by the presence of dirty, matted belly

TABLE 3. Mean T_e , T_n , and T_a when Wilson's Plovers cooled their eggs or nest by shading or sitting (1981 data) or by belly soaking (1980 data).^a

During:	T_e	T_n	T_a
Shading	37.1 ± 0.9 (35.2–38.5, 12)	34.9 ± 1.4 (31.5–37.5, 12)	34.4 ± 2.1 (29.7–36.5, 12)
Sitting	39.1 ± 0.7 (38.5–39.9, 3)	36.5 ± 1.1 (35.4–37.5, 3)	37.0 ± 1.7 (36.0–39.0, 3)
Belly soaking	—	41.8 ± 1.6 (38.9–44.2, 11)	38.3 ± 3.2 (33.6–45.3, 11)
All data, 1980 ^b	—	37.2 ± 3.4 (27.1–48.5, 605)	34.3 ± 3.8 (23.9–45.3, 605)

^a $\bar{x} \pm \text{SD}$ (min–max, n).

^b Only daylight data from the four nests at which belly soaking occurred. See Table 1 for daylight means for shading/sitting data (1981).

feathers, which were visible as the parent crouched over the eggs. During 750 hr of observation at 13 nests in 1980, four different pairs of Wilson's Plovers used belly soaking 24 times, with 15 uses by one pair. It occurred one to three times per day at these nests. All cases of belly soaking were at nests on pavement, probably the hottest substrate; all were in June, the hottest month in which I collected data; and all occurred between 11:47 and 18:57, the hottest part of the day. I studied only one pair nesting on pavement in June that did not use belly soaking, and its eggs were hatching when I observed it. Belly soaking occurred at nest relief in 17 of 24 cases, and hatching changed nest-relief patterns (Bergstrom 1982), so this may have stopped belly soaking.

Belly soaking lowered T_n by $1.7 \pm 2.0^\circ\text{C}$, causing a drop in T_n in 11 of the 13 cases measured. Presumably it lowered T_e as well. In the two cases when T_n rose after belly soaking, T_n had been low, 36.0°C , when it began. Mean T_e , T_n , and T_a during episodes of egg or nest cooling (Table 3) show that under warming conditions, parents used shading, sitting, and then belly soaking to cool the eggs. Belly soaking has never been reported in Wilson's Plovers, but it has been seen by several authors in Killdeers (Grant 1982).

Why wasn't belly soaking more common at Wilson's Plover nests in Texas? Its limitation to nests on pavement suggests that the maximum T_e or T_a was not high enough to require it at nests on soil. Whether the nests were too far from water to permit it more often is unclear. Some of the nests where belly soaking occurred were 0.5 km from the nearest permanent water (Bergstrom 1988), while Snowy Plovers at the Salton Sea nested 10 m from water (Grant 1982). Nests were probably far from water because of the risk of nest loss from flooding (Bergstrom 1988). The distance of nests from water might limit the parents to using belly soaking at nest relief, since the eggs could overheat if left uncovered while they flew that far to belly soak. However, belly soaking did not follow nest relief in seven of 24 cases. In those seven cases, the parent spent more time off the nest when T_a was lower: as little as 2.1 min (when $T_a = 45.3^\circ\text{C}$) or as much as 30.2 min (when $T_a = 33.6^\circ\text{C}$).

CONCLUSIONS

Incubation in these two plovers functions both to cool and to warm the eggs. This is shown by

the parents' variation in attentiveness with T_a , and the drops in T_e and T_n caused by shading, sitting, and belly soaking. The regulation of T_e was less than perfect, as shown by the positive slopes of the regressions of T_e and T_n on T_a , and there was less regulation (higher slopes) at unlined pavement nests than at lined soil nests in Wilson's Plovers. Wilson's Plovers switched from using shading to using sitting to cool their eggs when T_e exceeded 38°C . Most Wilson's Plovers and Killdeers regulated T_e within safe limits with these behaviors without using belly soaking, but Wilson's Plovers nesting on pavement used belly soaking when T_n and T_a were very high. Wilson's Plovers may avoid needing belly soaking by nesting where T_a levels do not require it, and belly soaking may be infrequent when it occurs because nesting near water increases the risk of nest flooding.

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