

INCUBATION TEMPERATURES AND BEHAVIOR OF CROWNED, BLACK-WINGED, AND LESSER BLACK-WINGED PLOVERS

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ABSTRACT.—Crowned Plovers (*Vanellus coronatus*), Black-winged Plovers (*V. melanopterus*), and Lesser Black-winged Plovers (*V. lugubris*) incubate their eggs during early spring in short unshaded grasslands and open woodlands. I studied incubation behavior in hot environments and the ability to control brood-patch temperatures. Crowned and Black-winged plovers kept brood-patch temperatures almost constant, while the temperature of Lesser Black-winged Plovers was more poorly controlled, probably as a result of a large body surface area-to-volume ratio. At high ambient temperatures, Crowned and Black-winged plovers shaded their eggs more than did Lesser Black-winged Plovers. Lesser Black-winged Plovers controlled nest-air temperatures at high ambient temperatures by frequent shifts in nest attendance by male and female, which allowed the nonsitting bird to cool in the shade. Received 30 January 1989, accepted 15 June 1989.

LIKE all *Vanellus* species (Charadriiformes: Vanellinae), Crowned Plovers (*V. coronatus*), Black-winged Plovers (*V. melanopterus*), and Lesser Black-winged Plovers (*V. lugubris*) are ground-nesters. The three species are widely distributed (Maclean 1985). They nest in areas of short or burnt grass in open grasslands or open woodlands far from bodies of water, usually during late winter or early spring. Nests are scrapes on the ground and have no cover to shield incubating birds from the elements. Virtually all previous studies of ground-nesting birds in hot environments (except Maclean 1967, 1976) have dealt with species that nest near water and have described the bird's use of water to decrease egg temperatures during hot periods (e.g. Jayakar and Spurway 1965, Howell 1979, Grant 1982).

I examined the responses of the incubating adults, and their eggs, to insolation. The effects of body size on incubation could be included because two species were of similar size (Crowned Plover: mass = 160–200 g, \bar{x} = 167 g; Black-winged Plover: mass = 160–175 g, \bar{x} = 167 g) and larger than the Lesser Black-winged Plover (mass = 107–130 g; \bar{x} = 121 g) (Ward 1987).

MATERIALS AND METHODS

I compared the incubation temperatures and associated behavior of the three plover species by detailed observation of nests over the entire incubation period, at the expense of studying many nests of each species. Incubation temperatures were recorded in one pair of Crowned Plovers in Pietermaritzburg, Natal, South Africa (29°30'S, 30°30'E), and three pairs at Ndumu, Natal, South Africa (28°30'S, 32°45'E), three pairs of Black-winged Plovers in Pietermaritzburg, and three pairs of Lesser Black-winged Plovers at Ndumu. All nests studied were successful. Plovers were nest-trapped (Sordahl 1980) and were marked individually with color bands. In 1985 and 1986, incubation temperatures at each nest were measured mostly during the day (sunrise to sunset) and for a single night (1800–0600). I measured temperatures with a Yellow Springs Instruments telethermometer placed in a blind 10 m from the nest and equipped with three thermistor probes that were calibrated to $\pm 0.1^\circ\text{C}$ against a standard thermometer. Nest-air temperature was measured between the eggs on the floor of the nest. To measure brood-patch temperature, I placed a second probe on top of a plaster-of-paris model painted to resemble a plover egg. I secured the model in place to prevent the birds from turning it. The thermal conductivity (watt per meter Kelvin) of plaster-of-paris ($0.432 \text{ W}\cdot\text{m}^{-1}\cdot\text{K}^{-1}$, Weast 1986) is the same as that of an authentic egg ($0.43 \text{ W}\cdot\text{m}^{-1}\cdot\text{K}^{-1}$, Henderson 1963), so the buffering effect on the recorded brood-patch temperatures is likely to be similar to a natural egg. The third probe, to measure ambient temperature, was placed 1 m from the nest and 5 cm above ground. The external probe was painted with a white reflective paint and was not shaded. This produced the most accurate measurement of air temperature in the field,

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with small error due to radiation and without the problem of inadequate ventilation experienced by shaded probes (Christian and Tracy 1985). I measured wind speed with an anemometer outside the blind, hand-held 5 cm above ground. Temperature and wind-speed readings were taken every 15 min. Observations at night were made with a light-intensifying telescope.

The time that the nest was occupied by either partner was *nest attendance*. I compared the amount of time that the nest was attended among 10°C ambient-temperature ranges.

The amount of time that the nest was occupied by a particular individual was *nest attentiveness*. I compared the changes in an individual's contribution to incubation relative to the total time that the nest was attended among 10°C ambient-temperature ranges. I scored the length of incubation shifts by each individual within each 10°C ambient-temperature range. The number of observations equaled the number of incubation shifts per individual within a particular 10°C range. Comparisons were made of the relative contributions of males and females to incubation in different 10°C ambient-temperature ranges. A Wilcoxon test (Zar 1974) was used because the presence of the male and female on the nest is negatively correlated, which precludes the use of a parametric test.

I analyzed *shading behavior* using the proportion of time that the birds shaded the egg relative to the total time that ambient temperatures were in a particular 5°C range. All data for nest attendance, attentiveness (except comparisons between male and female), and shading behavior were arcsine transformed (Zar 1974), with the number of observations equal to the number of hours or parts thereof (minimum of 30 min) that ambient temperature fell within a particular temperature range.

The amount of time that a particular individual remained on a nest before being relieved by its partner was *incubation-bout duration*. The number of observations equals the number of incubation bouts within a particular 10°C temperature range.

RESULTS

Crowned Plovers.—All Crowned Plovers studied were monogamous. I followed the incubation of seven Crowned Plover pairs from the laying of the last egg of the clutch until the hatching of the last egg, but I measured incubation temperatures at only four of these nests.

The four Crowned Plover pairs at Pietermaritzburg initiated incubation only after clutch completion. The three pairs at Ndumu started to incubate after laying the first egg. Incubation ranged from 29–31 days. Brood-patch temperatures of Crowned Plovers increased with am-

bient temperature, and ranged from 26.2°C to 45°C ($\bar{x} \pm \text{SE} = 37.54 \pm 0.17^\circ\text{C}$ at Ndumu, $n = 161$; and $35.52 \pm 0.29^\circ\text{C}$ at Pietermaritzburg, $n = 101$). The best-fit curve of brood-patch temperature on ambient temperature for the pair at Pietermaritzburg was $y = 1/(0.04 - 0.01x)$; $r^2 = 0.39$ ($P < 0.01$, $n = 101$). This was significantly different from that of the three pairs of Crowned Plovers at Ndumu (Table 1; ANCOVA, $P < 0.05$).

Nest-air temperatures of Crowned Plovers were $31.90 \pm 0.33^\circ\text{C}$ (Pietermaritzburg) and $33.29 \pm 0.25^\circ\text{C}$ (Ndumu) (Table 1). The temperature difference between brood patch and nest air decreased from 9°C at ambient temperature 13°C to 1°C at ambient temperature 50°C.

Female Crowned Plovers did most daytime incubation over the range of temperatures measured (Wilcoxon test, $P < 0.05$), and they did all nighttime incubation (Fig. 1). Males spent significantly less time incubating at air temperatures $< 20.1^\circ\text{C}$ than at any other range of ambient temperatures (ANOVA, $P < 0.05$).

Nest attendance by both sexes increased significantly at air temperatures $< 20^\circ\text{C}$ and $> 40^\circ\text{C}$ (ANOVA, $P < 0.05$; Fig. 2), although the total time spent at the nest varied considerably (one pair at Pietermaritzburg spent 61.2% of the time off the nest, largely as a result of human disturbance; the three pairs at Ndumu spent 22.2%, 18.2%, and 18.5% off the nest). Both parents vacated the nest during morning (0500–0700) and evening (1630–1800) feeding periods. At ambient temperatures $> 35^\circ\text{C}$, Crowned Plovers significantly increased the amount of time spent shading the eggs (Fig. 3) between successive 5°C ambient-temperature increments (ANOVA, $P < 0.05$); but they did not shade when the wind speed was $> 3 \text{ m}\cdot\text{s}^{-1}$. Shading behavior involved squatting on the tibiotarsal joints with the body raised ca. 2 cm above the eggs. In addition, the crown, neck, and mantle feathers were raised; the wings were drooped so that the wrist was below the level of the belly; and the eyes swelled (the pupil was dilated and, when the bird was viewed from the front or behind, the eyes protruded more than usual) and took on a glazed appearance. The lowest air temperatures were 37.2°C for feather ruffling, 39.8°C for bill gaping, and 47.7°C for gular fluttering. Bill gaping grades into panting (thermal hyperpnea) in the Charadriiformes (Grant 1982), so the onset of bill gaping was used as an in-

TABLE 1. Brood-patch, nest-air, and air temperature of Crowned, Black-winged, and Lesser Black-winged plovers.

Species	Regression	Best-fit curve	r^2	$s_{y,x}$	Significance	df
Crowned Plover	Brood-patch vs. air	$y = 0.15x + 32.00$	0.22	1.88*	$P < 0.01$	161
	Nest-air vs. air	$y = 0.37x + 19.82$	0.56	2.18	$P < 0.01$	161
Black-winged Plover	Brood-patch vs. air	$y = 0.03x + 36.68$	0.12	0.88	$P < 0.01$	226
	Nest-air vs. air	$y = 9.36(\log x) + 0.40$	0.83	0.06	$P < 0.01$	226
Lesser Black-winged Plover	Brood-patch vs. air	$y = 0.28x + 27.42$	0.53	2.62	$P < 0.01$	195
	Nest-air vs. air	$y = 0.28x + 23.69$	0.65	2.07	$P < 0.01$	195

* Standard error of the estimate, an unbiased estimate of the variance in the regression equation.

indicator of heat stress. At high ambient temperatures (above ca. 35°C), Crowned Plovers secreted a saline secretion (determined by taste) from their nostrils. In cold weather, these plovers (like Black-winged and Lesser Black-winged plovers) also raised the feathers of the crown, neck, and mantle, but they layered them so that the distal tip of one feather touched the feather beneath it.

Nest relief was controlled by the female, which frequently left the nest if the male did not respond to her nest-relief call. Males did not make any nest-relief call. At nest relief, the sitting bird rose and walked 5 cm from the nest, then picked up bits of dry or burnt grass and tossed them into the nest, and then walked about 1 m while continuing to throw pieces of grass. This throwing behavior was frequently performed without actually picking up an object. The relieved bird then walked away from the nest and stood in the shade (if ambient temperature was high, i.e. above ca. 30°C), or fed (if the ambient temperature was moderate, i.e. below ca. 28°C). When the sitting bird rose, the relieving bird walked to within 2 m of the nest and tossed grass sideways. It then walked to the nest, rearranged grass around it, and rearranged the eggs before sitting on them.

The duration of incubation bouts (between incubation shifts) varied considerably within each 10°C ambient-temperature group (Fig. 4), with no significant difference among groups (ANOVA, $P > 0.05$). Incubation-bout duration ($\bar{x} \pm SE$) was 92.0 ± 7.10 min.

Black-winged Plovers.—All Black-winged Plovers studied were monogamous. Incubation began after clutch completion unless air temperatures rose above ca. 30°C prior to clutch completion. Then, incubation occurred until temperatures dropped below ca. 30°C. The incubation period of six pairs of Black-winged

Plovers ranged from 30–31 days. Black-winged Plovers maintained an almost constant brood-patch temperature regardless of ambient temperature (Table 1). The slope of the regression of brood patch on ambient temperature was significantly steeper in Crowned Plovers than in Black-winged Plovers (ANCOVA, $P < 0.001$). Nest-air temperatures increased logarithmically in the range of ambient temperatures (12.6–50.1°C; Table 1), such that the temperature difference between brood patch and nest air decreased from 15.1°C at 12.6°C to 1°C at 50.1°C. The temperature of the brood patch was $38.60 \pm 0.06^\circ\text{C}$, and the nest-air temperatures were $30.83 \pm 0.27^\circ\text{C}$.

Males incubated significantly longer (ANOVA, $P < 0.05$) at lowest ($< 20.1^\circ\text{C}$) and highest ($> 40^\circ\text{C}$) air temperatures than at intermediate temperatures, and significantly longer than females at air temperatures $> 40^\circ\text{C}$ (Wilcoxon test, $P < 0.05$; Fig. 1). Females incubated significantly longer than males in all other temperature ranges (Wilcoxon test, $P < 0.05$). Only females incubated at night, and they controlled nest relief by day. Nest-relief behavior followed the pattern described for Crowned Plovers. Black-winged Plovers left the nest unoccupied for 11.6% of the total time that nests were observed (Fig. 2). Black-winged Plovers did not vacate the nest to feed as did Crowned Plovers, but Black-winged Plovers took turns feeding and incubating.

Incubation-bout duration did not vary significantly over the temperature range (ANOVA, $P > 0.05$; Fig. 4). Incubation-bout duration was 92.79 ± 10.71 min. Shading behavior increased significantly with each 5°C increment in air temperature (ANOVA, $P < 0.05$; Fig. 3), although Black-winged Plovers did not shade when the wind speed was $> 3 \text{ m}\cdot\text{s}^{-1}$. Black-winged Plovers started feather ruffling at 35.8°C,

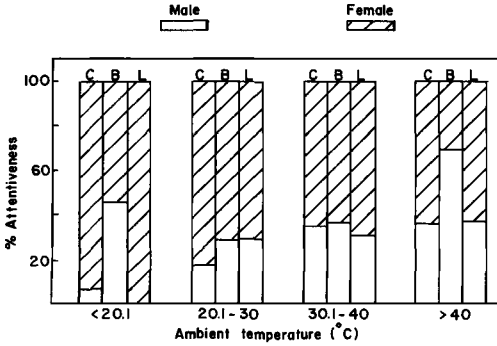


Fig. 1. Nest attentiveness in Crowned Plovers (C), Black-winged Plovers (B), and Lesser Black-winged Plovers (L) as a percentage of total time spent by male and female on the nest in each air temperature category ($n = 372$ [C], 153 [B], and 171 [L] hours of observation).

bill gaping at 36.6°C, and gular fluttering at 40.8°C. A saline solution (determined by taste) was exuded from the nostrils at temperatures above ca. 35°C. At air temperatures >44.5°C, the birds uttered "tiow-tiow" calls and intermittently changed position on the nest.

Lesser Black-winged Plovers.—All Lesser Black-winged Plovers studied were monogamous and initiated incubation immediately after laying the first egg. The incubation period of the four pairs studied ranged from 27–28 days. Brood-patch temperatures increased with increased air temperatures over the range (17.0–50.6°C) of air temperatures ($\bar{x} \pm SE = 37.78 \pm 0.27^\circ\text{C}$; Table 1). The slope of the regression of brood patch on ambient temperature for Lesser Black-winged Plovers was significantly steeper than that of Crowned Plovers (ANCOVA, $P < 0.001$). Nest-

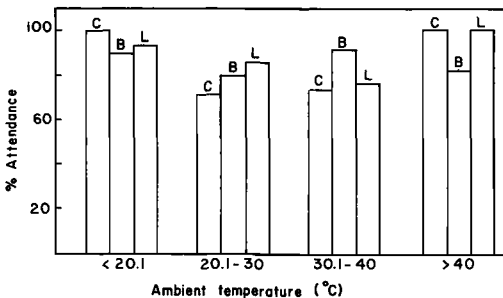


Fig. 2. Nest attendance relative to air temperature as a percentage of the total time spent observing three pairs of Crowned (C), Black-winged (B), and Lesser Black-winged (L) plovers ($n = 372$ [C], 153 [B], and 171 [L] hours of observation).

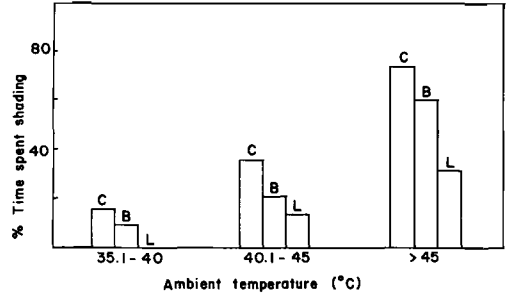


Fig. 3. Time spent shading eggs relative to ambient temperature as a percentage of total time spent observing three pairs of Crowned (C), Black-winged (B), and Lesser Black-winged (L) plovers ($n = 167$ [C], 24 [B], and 107 [L] hours of observation).

air temperatures also increased with increased ambient temperatures (Table 1) with a mean nest-air temperature of $34.11 \pm 0.25^\circ\text{C}$. The difference between temperatures of brood patch and nest air remained constant at 3.7°C over the range of air temperatures.

Males did not incubate at night or at air temperatures below 20°C . Females incubated significantly longer than males in all temperature ranges (Wilcoxon test, $P < 0.05$). There was no significant change in nest attentiveness by males among the three ambient temperature classes from 20.1–40°C (ANOVA, $P < 0.05$; Fig. 1). Mean incubation-bout duration was 40.12 ± 4.15 min (Fig. 4), and it decreased significantly at temperatures >40°C (ANOVA, $P < 0.05$). Males controlled incubation in this species, relieving

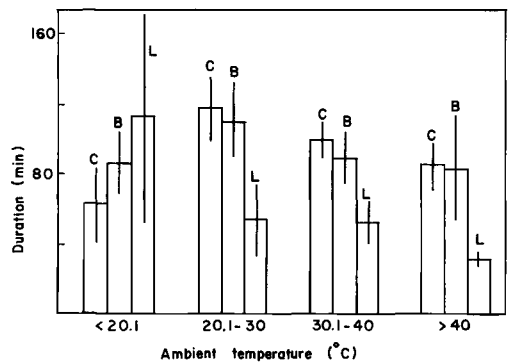


Fig. 4. Incubation-bout duration relative to air temperature in three pairs of Crowned (C), Black-winged (B), and Lesser Black-winged (L) plovers. Vertical lines = 95% confidence limits; bars indicate mean values; $n = 306$ (C), 99 (B), and 258 (L) total bouts.

females at the nest without females vocalizing, but females responded to males' soft, low-frequency "tiu" calls for nest relief. These calls were given intermittently for ca. 1 min before the female responded. The off-duty bird walked to within ca. 10 cm of the nest and waited until the incubating bird stood. While standing, the on-duty bird began to throw bits of grass without moving away from the nest. The throwing behavior appeared more vigorous in these birds than in Crowned and Black-winged plovers because the bird threw small pieces of grass up to 20 cm. The incoming bird sat under the tail (if it approached from the back) or under the belly (if it approached from the front) of the departing bird, which continued to throw pieces of grass (while walking away from the nest) for about 1 min after being relieved. The relieved bird then moved off to stand in the shade.

Nest attendance by Lesser Black-winged Plovers increased significantly (ANOVA, $P < 0.05$) at air temperatures $>40^{\circ}\text{C}$ (Fig. 2). Both parents vacated the nest to feed in the mornings (0430–0700), but one remained on the nest in the afternoons. Six pairs nesting together in a loose colony in Ndumu (1985) left the nesting area simultaneously each morning to feed at Mandlankunse pan about 5 km south of the breeding area. In the afternoons, the incubating birds relieved one another at the nest. This allowed the off-duty bird to feed. Lesser Black-winged Plovers spent significantly less time shading (ANOVA, $P < 0.05$) at temperatures $>45^{\circ}\text{C}$ than Crowned and Black-winged plovers (Fig. 3). Lesser Black-winged Plovers did not shade their eggs at temperatures $<40^{\circ}\text{C}$ and, at air temperatures $>45^{\circ}\text{C}$, shaded the eggs for only 31.2% of the time. The lowest air temperatures at which Lesser Black-winged Plovers started feather ruffling, bill gaping, and gular fluttering were 36.7°C , 39.8°C , and 43.0°C , respectively. Lesser Black-winged Plovers exuded a saline solution (determined by taste) from the nostrils at ambient temperatures above ca. 35°C . At air temperatures above ca. 45°C , Lesser Black-winged Plovers had wet legs. This liquid was tasteless and left no residue on the legs upon drying.

DISCUSSION

Brood-patch and nest-air temperatures.—Nest temperatures result from the interaction of

thermal conduction from the soil and heat produced by the incubating bird. The difference between brood-patch and nest-air temperatures provides an indication of the difference in temperature across the egg. I did not attempt to determine embryo temperature, which is a function of metabolic heat production and exchanges caused by radiation, latent heat of evaporation, convection and conduction (Webb and King 1983). The advantage of the method I used over implantation of a thermocouple or thermistor in a natural egg (e.g. Vleck 1981, Grant 1982) is to eliminate the confounding effect of metabolic heat production, which changes with the developmental stage of the embryo.

The regression of brood-patch temperature against air temperature in Crowned Plovers had a low slope, indicating a considerable degree of control of brood-patch and therefore egg temperature. The difference in the brood-patch/ambient temperature regression in Crowned Plovers between Ndumu and Pietermaritzburg implies a considerable amount of intraspecific variation in brood-patch temperatures in this species. This variation may be related either to the degree of control of brood-patch temperature exerted by the adult or to intraspecific variation in the tolerance of the embryos to temperature changes. Further examination of intraspecific variation in the control of brood-patch temperature and embryo tolerance of temperature changes at a wider range of localities is required.

Black-winged Plovers kept brood-patch temperatures relatively constant regardless of air temperature. This species is largely restricted to cooler highland areas and may be intolerant of high temperatures. As a result, these birds may need to expend more energy in metabolic heat production at lower temperatures and to use behavioral mechanisms (e.g. panting, feather ruffling, and gular fluttering) at higher temperatures to maintain a constant brood-patch temperature. Nest-air temperatures in this species declined sharply at lower ambient temperatures. Presumably, soil-surface temperatures were lower than in the other study species and may be related to the thermal conductivity of the soil type where the birds were nesting. The selection of nest microhabitat requires further examination because the thermal conductivity of the soil in the nest vicinity may help control egg temperatures, as has been shown in

other bird species (Ackerman and Seagrave 1987). The Black-winged Plover was the only one of the three study species in which males increased the time spent incubating at low as well as at high temperatures. This may be related to the low nest-air temperatures at low air temperatures. Males relieve females to allow the females to restore their body temperature by standing, which reduces body surface area in contact with the cool soil.

Lesser Black-winged Plovers exhibited less control of brood-patch temperature than the other two species, because the slope of the regression of brood-patch temperature on ambient temperature was much steeper and showed no sign of attenuation at high or low temperatures. The brood-patch temperature was higher than in the other two species without any detrimental effect on embryo survival. This low degree of control is likely to be related to the relatively small body size and, consequently, large body surface area-to-volume ratio, which causes rapid changes in temperature. Smaller birds have less feather insulation, gain and lose heat more quickly, and therefore have less control over their body temperatures (Kendeigh 1970).

Nest attendance and attentiveness.—All three species initiated incubation prior to the completion of the clutch if air temperatures were high. This did not cause hatching asynchrony (Ward 1987), presumably because the amount of time spent incubating at these temperatures was insufficient to advance embryo growth in the older eggs.

Crowned Plovers can spend long periods off the nest without the embryos dying (Fig. 2). This may allow the parents to feed and maintain their body reserves even in times of low food supply. In addition, the parent may be able to leave the nest for extended periods to avoid attracting a predator's attention to the eggs. I found no anti-predatory advantage to remaining away from the eggs. Hatching success in Crowned Plovers (79%) was less than hatching success in Black-winged Plovers (96%), which spent very little time away from the nest. It was, however, greater than hatching success in Lesser Black-winged Plovers (58%) (Ward 1987).

Males of all three species incubated, and they increased incubation at higher air temperatures. I assumed that males are required to relieve females at the nest at high ambient tem-

peratures (supported by increased nest attentiveness by males of all three species and decreased incubation-bout durations in Lesser Black-winged Plovers) to allow the female to lower body temperature by standing in the shade. Incubation may not be energetically demanding to the males (Norton 1972, Maxson and Oring 1980) because they spend less time incubating than the females, but it may severely curtail the male's time (Fig. 1) for other activities, such as foraging. This may be the most important factor limiting polygyny in the Vanellinae. The long periods that Crowned Plovers may be able to leave the nest unattended, together with the relatively short time that the male incubates, may allow these birds to become polygynous on occasion, as was found in one instance at Pietermaritzburg (Ward 1987), and as has been recorded in other Vanellinae (Wilson 1967, Walters and Walters 1980).

Adaptations to high temperatures.—I found that the control of egg temperature during periods of high ambient temperature is of primary importance to the incubation biology of these species. In all three species, elevating the feathers increased the insulation in the cold and promoted convective cooling during hot periods. At the same time, it reduced heat gain by solar radiation (Whittow 1986). In addition, cutaneous evaporation is probably enhanced in the heat. Marder and Ben-Asher (1983) found that the cooling capacity of cutaneous water evaporation ranged from 17% (Japanese Quail, *Coturnix c. japonica*) to 96.5% (Rock Dove, *Columba livia*) of metabolic heat during heat stress (>45°C). However, Lasiewski et al. (1971) determined that cutaneous evaporation accounted for slightly more than 45% of the total evaporative water loss in nine species of birds. This water loss results in the buildup in the body of salts, which are then excreted via nasal glands (Grant 1982).

The glazed, swollen appearance of the eyes of all three species during hot periods may be associated with the functioning of a *rete ophthalmicum*. This system provides countercurrent cooling of arterial blood flowing toward the brain and, in Rock Doves, keeps the brain cooler than the body core (Pinshow et al. 1982).

The legs of Crowned and Black-winged plovers became redder during incubation. This suggests an increased blood supply, which possibly facilitated cooling. The legs of Lesser Black-

winged Plovers are black so an increased blood supply to the legs is unlikely to be perceived as a color change. Lesser Black-winged Plovers, unlike the other two species, had wet legs during the heat of the day. Because birds do not have exocrine (sweat) glands (Yapp 1970), it is likely that urine was used to cool the legs and to lower the body temperature. This liquid was tasteless and left no exudate after drying. If urine was used, it was very dilute. This behavior was recorded in Marabou Storks (*Leptoptilos crumeniferus*; Kahl 1963), whose legs are coated white by excreta. It is not clear why a bird that excretes excess salt through nasal glands would excrete dilute urine, which represents a potential water loss, onto its legs.

Both panting and gular flutter cause a significant loss of heat by evaporation. Over prolonged periods, they can cause respiratory alkalosis and high total evaporative water loss (Whittow 1986). Crowned, Black-winged, and Lesser Black-winged plovers initiated panting and gular flutter at higher air temperatures (minimum 5°C) than five species of charadriiform birds nesting in a hot environment near the Salton Sea, California (Grant 1982). Presumably, Crowned, Black-winged, and Lesser Black-winged plovers are more tolerant of high ambient temperatures and are better able to reduce energy expenditure and total evaporative water loss. Black-winged Plovers initiated bill gaping, feather ruffling, and gular fluttering at lower ambient temperatures than Crowned and Lesser Black-winged plovers, which supports the hypothesis that Black-winged Plovers are less tolerant of high temperatures.

Egg shading occurs when increased body temperature reduces the ability of the brood patch to control egg temperature adequately (Grant 1982). All three species stopped shading and sat on their eggs in windy conditions at high air temperatures. Wind breaks up the boundary layer of relatively cool air between bird and eggs, it blows air across the eggs from the warm ground around the nest, and it thus increases egg temperature (Purdue 1976). The plovers may have responded to the increased egg temperature sensed by the legs, which are in contact with the eggs.

Crowned Plovers had relatively long incubation bouts and started gular fluttering at higher temperatures than the other two species. This suggests that they experienced less thermal stress during incubation. Lesser Black-

winged Plovers spent less time shading their eggs at high air temperatures than did the other two species, but they relieved mates more frequently and controlled brood-patch temperatures more closely. This difference in behavior is probably related to the large body surface area-to-volume ratio of the smaller Lesser Black-winged Plovers. The two larger species probably cool more slowly in the shade between incubation bouts, but they also do not heat as quickly on the nest in the sun. As a result, they have longer bouts of incubation. Lesser Black-winged Plovers, which gain heat quickly on the nest and lose heat quickly in the shade, exchanged positions on the nest more frequently.

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LITERATURE CITED

- ACKERMAN, R. A., & R. C. SEAGRAVE. 1987. Modelling heat and mass exchange of buried avian eggs. *J. Exp. Zool. Suppl.* 1: 87-97.
- CHRISTIAN, K. A., & C. R. TRACY. 1985. Measuring air temperature in field studies. *J. Therm. Biol.* 10: 55-56.
- GRANT, G. S. 1982. Avian incubation temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithol. Monogr.* 30.
- HENDERSON, S. M. 1963. On-the-farm egg processing, part 3: thermal conductivity, generalized cooling procedure and cooling in water. *Trans. Am. Soc. Agric. Eng.* 6: 95-97.
- HOWELL, T. R. 1979. Breeding biology of the Egyptian Plover, *Pluvianus aegyptius*. Berkeley, Univ. California Press.
- JAYAKAR, S. D., & H. SPURWAY. 1965. The Yellow-wattled Lapwing, *Vanellus malabaricus* (Boddaert), a tropical dry-season nester: II. Additional data on breeding biology. *J. Bombay Nat. Hist. Soc.* 62: 1-14.
- KAHL, M. P. 1963. Thermoregulation in the Wood Stork, with special reference to the role of the legs. *Physiol. Zool.* 36: 141-150.
- KENDEIGH, S. C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72: 60-65.
- LASIEWSKI, R. C., M. H. BERNSTEIN, & R. D. OHMART. 1971. Cutaneous water loss in the Roadrunner and Poor-will. *Condor* 73: 470-472.

- MACLEAN, G. L. 1967. The breeding biology of the Double-banded Courser *Rhinoptilus africanus* (Temminck). *Ibis* 109: 556-569.
- . 1976. A field study of the Australian Pratincole. *Emu* 76: 171-182.
- . 1985. Roberts' birds of southern Africa. Cape Town, John Voelcker Bird Book Fund.
- MARDER, J., & J. BEN-ASHER. 1983. Cutaneous water evaporation: I. Its significance in heat-stressed birds. *Comp. Biochem. Physiol.* 75A: 425-431.
- MAXSON, S. J., & L. W. ORING. 1980. Breeding season, time and energy budgets of the polyandrous Spotted Sandpiper. *Behavior* 74: 200-263.
- NORTON, D. W. 1972. Incubation schedules of four species of calidrine sandpipers at Barrow, Alaska. *Condor* 74: 164-176.
- PINSHOW, B., M. H. BERNSTEIN, G. E. LOPEZ, & S. KLEINHAUS. 1982. Regulation of brain temperature in pigeons: effects of corneal convection. *Am. J. Physiol.* 242: R577-R581.
- PURDUE, J. R. 1976. Thermal environment of the nest and related parental behavior in Snowy Plovers, *Charadrius alexandrinus*. *Condor* 78: 180-185.
- SORDAHL, T. A. 1980. A nest trap for recurvirostrids and other ground-nesting birds. *North American Bird Bander* 5: 1-3.
- VLECK, C. M. 1981. Hummingbird incubation: female attentiveness and egg temperature. *Oecologia* 51: 199-205.
- WALTERS, J. R., & B. F. WALTERS. 1980. Cooperative breeding in Southern Lapwings *Vanellus chilensis*. *Ibis* 122: 505-509.
- WARD, D. 1987. The biology and systematic relationships of Crowned, Blackwinged and Lesser Blackwinged plovers. Ph.D. dissertation, South Africa, Univ. Natal.
- WEAST, R. C. (ED.). 1986. CRC handbook of chemistry and physics. Boca Raton, Florida, CRC Press.
- WEBB, D. R., & J. R. KING. 1983. An analysis of the heat budgets of the eggs and nest of the White-crowned Sparrow (*Zonotrichia leucophrys*) in relation to parental attentiveness. *Physiol. Zool.* 56: 493-505.
- WHITTOW, G. C. 1986. Regulation of body temperature. Pp. 221-252 in *Avian physiology* (P. D. Sturkie, Ed.). New York, Springer-Verlag.
- WILSON, J. 1967. Trigamy in Lapwing. *Brit. Birds* 60: 217.
- YAPP, W. B. 1970. The life and organization of birds. London, Edward Arnold.
- ZAR, J. H. 1974. Biostatistical analysis. Englewood Cliffs, New Jersey, Prentice-Hall.