

## DOES SHADING BEHAVIOR OF INCUBATING SHOREBIRDS IN HOT ENVIRONMENTS COOL THE EGGS OR THE ADULTS?

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**ABSTRACT.**—Birds that nest on the ground in hot environments employ behavioral and physiological mechanisms to prevent the overheating of their eggs and themselves (e.g. egg covering, belly soaking, orientation on the nest, ptiloerection, panting, and gular fluttering). One of the least energetically expensive behaviors employed during incubation at high temperatures is nest shading. During shading, the birds raise themselves onto their tibiotarsi so that the incubation patch is about 2 to 3 cm above the eggs. It has frequently been assumed that birds adopt shading behavior to allow for direct convective cooling of the eggs. However, an alternative hypothesis is that birds rise up onto their tibiotarsi in order to place themselves out of the boundary layer. In doing so, adult birds cool themselves directly by convection. The lowering of the adult's body temperature during nest shading may, of course, cool the eggs indirectly when the bird resumes incubation. We tested these hypotheses using a taxidermic model of a Crowned Plover (*Vanellus coronatus*), which nests in hot environments in South Africa. Field observations have shown that this species spends 20 to 50% of its time shading when incubating at high environmental temperatures. When we alternated the bird between incubating and shading positions, we found that bird temperature, but not egg temperature, was lowered by shading behavior. Furthermore, wind speed had a significant negative effect on bird temperature but not egg temperature. Therefore, our results support the hypothesis that shading behavior functions to lower the temperature of incubating adults rather than of the eggs. Received 24 September 1996, accepted 14 May 1997.

INCUBATION IN BIRDS usually is considered to be a warming process (e.g. Vleck 1981, Whitow 1986). However, bird species that nest on the ground in environments characterized by high daytime temperatures have to employ behavioral and physiological mechanisms to prevent the overheating of their eggs and themselves (Schmidt-Nielsen 1965, Grant 1982, Ward 1990). These mechanisms include egg covering (Maclean 1972), belly soaking (Jayakar and Spurway 1965, Howell 1979, Maclean 1975, Grant 1982, Ward 1988), orientation on the nest, ptiloerection, panting, and gular fluttering (Maclean 1967, 1975, 1976; Grant 1982; Ward 1989a,b). Eggshells of birds nesting in semiarid to arid regions also have reduced water-vapor conductance, increased thickness, and reduced effective pore area (Ar et al. 1974, Vleck et al. 1979, Ward 1987, Arad et al. 1988).

Attentive behavior at the nest is thought to be important for maintenance of egg tempera-

tures below lethal levels in harsh, hot environments (Grant 1982, Ward 1989a,b). During the heat of the day, incubating shorebirds nesting near the Salton Sea in California spent most of their time shading or loosely sitting over their eggs (Grant 1982). Nest relief occurred about every 10 to 15 min during the heat of the day (Grant 1982). Indeed, many shorebirds that nest in areas of high ambient temperatures shade their eggs at moderate to high temperatures (Maclean 1976, Ward 1989a,b).

The Crowned Plover (*Vanellus coronatus*) is a medium-sized shorebird (average body mass = 167 g; Maclean 1993) that commonly occurs in open grasslands and lightly wooded savannas in sub-Saharan Africa (Ward and Maclean 1989). The nest is a shallow scrape (1 to 2 cm deep) in the ground (Ward 1987). These ground nests may get cold at night, requiring the parent to incubate the eggs to keep them warm. A more stressful period for the incubating birds occurs during the main breeding season, when daytime surface temperatures usually exceed 50°C. During these periods, the eggs require cooling (Ward 1990). Typical egg temperatures in birds vary between 30 and 35°C, and hyperthermia evidently is more injurious to the de-

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veloping embryo than is hypothermia (Webb 1987).

Crowned Plovers exhibit a variety of behaviors to reduce egg temperatures during incubation. They orient themselves with their backs to the sun when ambient temperatures exceed 20°C, unless the sun is directly overhead and the wind greater than 3 m s<sup>-1</sup>, at which time they face into the wind (Ward 1990). When ambient temperatures exceed 35°C, Crowned Plovers straddle the nest, squatting on their tibiotarsi with the body raised 2 cm above the nest, thus shading their eggs. They also raise their crown, neck, and mantle feathers; lower their wings so that the wrist is below the level of the belly; and their eyes swell (a result of the functioning of the rete mirabile ophthalmicum; see Kilgore et al. 1979, Pinshow et al. 1982). At even higher temperatures (>40°C), Crowned Plovers pant, ruffle their feathers, and exhibit gular fluttering (Ward 1990). Crowned Plovers increase the amount of time spent engaged in shading behavior during incubation from less than 20% between 35 and 40°C, to about 75% at ambient temperatures above 45°C. These behaviors allow Crowned Plovers to maintain nest and incubation-patch temperatures below ambient temperatures during the heat of the day (Ward 1990).

Unlike many other shorebird species, Crowned Plovers have no access to water when incubating, and thus cannot use egg wetting (e.g. Maclean 1975; Ward 1989a,b) to cool their eggs. Also, on the hard substrates where these birds nest, they cannot cool the eggs by covering them with soft sand (see Maclean 1972, Howell 1979). Two other mechanisms, panting and gular fluttering, cause a significant loss of heat by evaporation. Over prolonged periods, however, these two mechanisms can cause respiratory alkalosis and high total evaporative water loss (Whittow 1986). Thus, egg shading is the primary behavior available to Crowned Plovers for cooling their eggs that is not physiologically expensive.

The thermoregulatory role of shading behavior in Crowned Plovers and other ground-nesting birds has been little studied (Grant 1982, Ward 1990). We hypothesized that shading behavior has evolved because: (1) the incubation patch becomes too hot and the bird risks overheating the eggs, or (2) the incubating bird itself gets too hot as a result of its close contact

with the ground surface. In the first case, shading behavior allows cool air to pass over the eggs and cool them (Purdue 1976, Grant 1982). In the second case, the incubating bird places itself into the layer of cooler air above the boundary layer and then returns to its eggs once it has cooled itself sufficiently. We tested these hypotheses using a taxidermic model of a Crowned Plover and an egg model. If the first hypothesis were correct, we expected a greater change in the temperature of the egg than in the temperature of the adult following shading behavior, whereas the reverse would be true if the second hypothesis were correct.

#### MATERIALS AND METHODS

We obtained a frozen Crowned Plover from the Transvaal Museum. The plover was skinned and stuffed with aluminum foil to form a taxidermic model. Such models have essentially the same thermal properties as live birds but are thermally passive (Walsberg and Weathers 1986). Both copper (e.g. Bakken 1980) and aluminum (e.g. Goodfriend et al. 1991, Ward and Pinshow 1995) have been used for constructing such models. Aluminum, like copper, has high thermal conductivity (3.0 W cm<sup>-1</sup> °C<sup>-1</sup>; Weast 1986). We did not produce replicate models because there is no interindividual variance in such physical models. A Crowned Plover egg was used to make a mold for a representative plaster-of-paris egg. The thermal conductivity of plaster-of-paris (0.432 W m<sup>-1</sup> K<sup>-1</sup>, Weast 1986) is the same as that of an authentic egg (Henderson 1963), so the buffering effect on the recorded incubation-patch temperatures is likely to be similar to that of a natural egg. The exterior of the egg was colored to resemble the true egg, which has a khaki ground color (hue 5Y, value and chroma 8/2; Munsell 1966) boldly spotted with black and gray (Ward 1987, Maclean 1993).

The operative environmental temperature ( $T_e$ ; measured using models) is the equilibrium temperature an organism would attain with no metabolic heat production or evaporative water loss and serves as a measure of heat load (Bakken 1976, 1980; see also Ward and Pinshow 1995, Goodfriend et al. 1991). All temperatures of models mentioned below represent  $T_e$ .

We performed experiments to determine: (1) the changes in temperature of an unshaded, exposed model egg; (2) both egg and bird temperatures when the plover model was placed in a loosely sitting position over the egg; and (3) both egg and bird temperatures when the plover model was alternated from the sitting position to a shading position on its tibiotarsi and vice versa (each 30 min). During the latter experiments 2 and 3, the position of the model

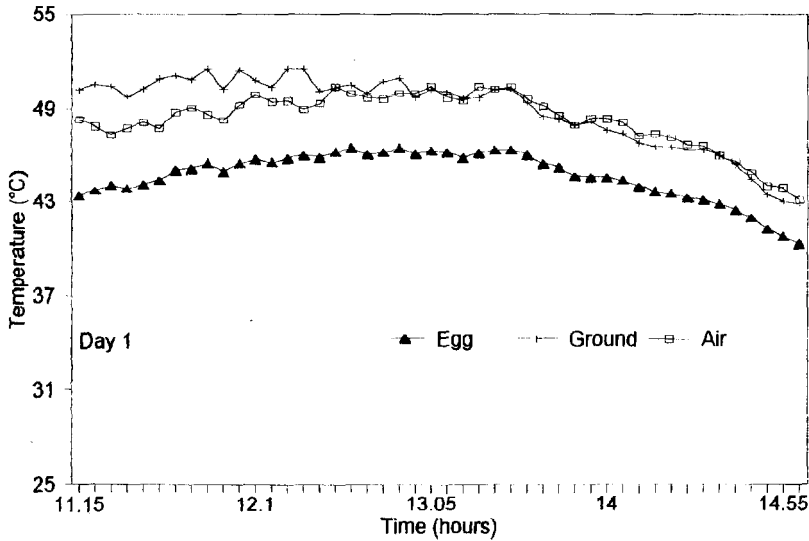


FIG. 1. Model plover egg temperature, together with air temperature and ground temperature, during experiment 1 when the egg was unshaded.

was changed so that it faced away from the sun, as these birds typically do under high insolation (Ward 1990).

We conducted experiments during September and October at KwaZulu-Natal, South Africa, in short grassland overlying a shale substrate. In this area, Crowned Plovers lay eggs from August until October (Ward 1989a). Each experiment began at 1100 and ended at 1500 and was repeated on three separate days when the weather was hot (maximum ambient temperature exceeding 35°C) and clear. Measurements were at 5-min intervals for experiments 1 and 2 and every minute for experiment 3. The air temperature 10 cm above ground, ground temperature next to the egg, and wind speed (12 cm above ground) were measured simultaneously using a data logger (Mik Cotton Systems, Cape Town, South Africa). We used copper-constant thermocouples to measure the internal thoracic-cavity temperature of the model and the internal egg temperature. Before use, probes were calibrated to  $\pm 0.1^\circ\text{C}$  against a standard thermometer.

## RESULTS

*Experiment 1: Egg alone.*—When the egg was exposed without shading from the bird, egg temperature was significantly lower than ground temperature ( $t = -4.7$ ,  $df = 137$ ,  $P < 0.001$ ) and air temperature ( $t = -10.3$ ,  $P < 0.001$ ; Fig. 1). The mean egg temperature was  $44.70 \pm \text{SE of } 0.31^\circ\text{C}$  (min.  $30.63^\circ\text{C}$ , max.  $49.98^\circ\text{C}$ ,  $n = 138$ ), and the mean air temperature measured simultaneously was  $46.94 \pm 0.30^\circ\text{C}$  (min.  $30.92^\circ\text{C}$ , max.  $51.06^\circ\text{C}$ ).

The simple regressions of egg temperature versus air temperature, ground temperature, and wind speed are shown in Table 1. When the temperature of the egg model was plotted against wind, there was a weak, but significant, correlation.

*Experiment 2: Egg shaded by the loosely sitting bird.*—When the egg was shaded by the loosely sitting bird for the duration of the experiment,

TABLE 1. Simple regression results when exposed egg temperature (i.e. no bird on egg) was plotted against air temperature, ground temperature, and wind speed.

Parameter	$r^2$	F	P	Intercept	Slope
Air temperature	0.55	168.12	<0.0005	8.90	0.76
Ground temperature	0.65	253.63	<0.0005	17.87	0.59
Wind speed	0.10	14.47	<0.0005	49.47	-2.98

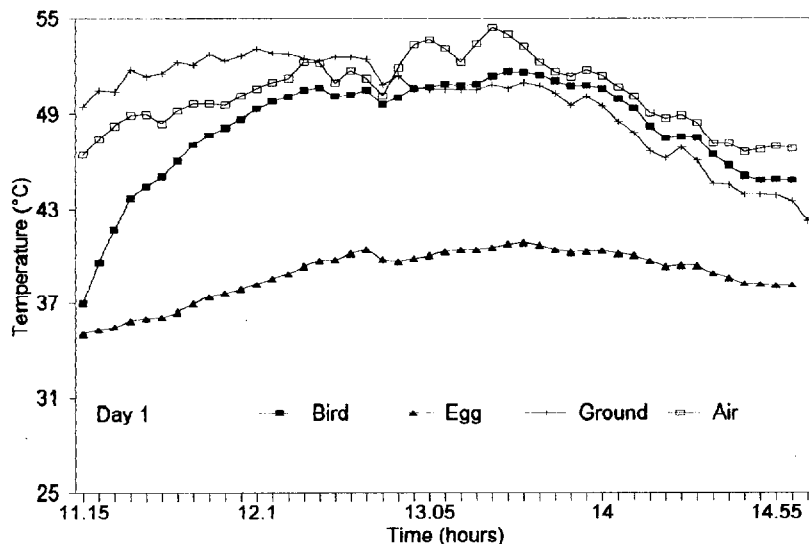


FIG. 2. Model plover body temperature when sitting loosely on the model egg showing change in egg temperature, together with air temperature and ground temperature, during experiment 2.

egg temperature was significantly lower than that of the bird ( $t = -51.9$ ,  $df = 137$ ,  $P < 0.001$ ), ground ( $t = -39.6$ ,  $P < 0.001$ ), and air ( $t = -36.1$ ,  $P < 0.001$ ; Fig. 2). The mean egg temperature was  $32.97 \pm 0.42^\circ\text{C}$  (min.  $24.74^\circ\text{C}$ , max.  $40.78^\circ\text{C}$ ,  $n = 138$ ). Mean air temperature and bird temperature measured simultaneously were  $43.50 \pm 0.53^\circ\text{C}$  (min.  $26.59^\circ\text{C}$ , max.  $54.46^\circ\text{C}$ ) and  $41.21 \pm 0.50^\circ\text{C}$  (min.  $27.82^\circ\text{C}$ , max.  $51.60^\circ\text{C}$ ), respectively.

We tested whether egg temperatures were lower (relative to air temperature) when covered by the continuously sitting bird than when the egg was exposed by subtracting air temperature from egg temperature for the two situations. Egg temperature was  $2.24 \pm 0.22^\circ\text{C}$  ( $n = 138$ ) lower than air temperature when the egg was exposed, and  $10.54 \pm 0.29^\circ\text{C}$  lower than air temperature when the bird was sitting on the egg ( $n = 138$  in each case). Thus, on average, the sitting bird reduced egg temperature relative to air temperature by about  $8^\circ\text{C}$ . This difference was highly significant ( $t = 24.3$ ,  $df = 137$ ,  $P < 0.001$ ).

*Experiment 3: Egg shaded by the bird raised off the egg at intervals.*—Air temperature and ground temperature were significantly positively correlated ( $r = 0.92$ ,  $P < 0.001$ ; Fig. 3). This correlation prevented us from using both variables as independent variables in our analyses. To avoid this problem, we used principal

components analysis to create a new variable that was a linear combination of ground and air temperature. The PC I axis explained 95% of the variance in these two variables. Therefore, we used PC I of air and ground temperatures (hereafter PCGA) to construct a new environmental temperature variable:

$$\text{PCGA} = 0.978(\text{ground temperature}) + 0.978(\text{air temperature}). \quad (1)$$

The temperature of the egg was not significantly affected by bird position (i.e. sitting on the egg vs. shading the egg; ANCOVA with PCGA and wind speed as covariates;  $F = 0.701$ ,  $df = 1$  and  $482$ ,  $P = 0.403$ ). The mean adjusted egg temperature was  $35.41 \pm 0.09^\circ\text{C}$  ( $n = 256$ ) when the bird was sitting on the egg and  $35.51 \pm 0.09^\circ\text{C}$  ( $n = 230$ ) when the bird was shading the egg.

A multiple regression with egg temperature as the dependent variable and wind speed, bird temperature, bird position (on or above the egg), and PCGA as the independent variables showed that there was a significant overall effect of these variables on egg temperature ( $F = 4,075.7$ ,  $df = 1$  and  $482$ ,  $P < 0.0005$ ). Regarding individual independent variables, only bird position, bird temperature, and PCGA had significant effects on egg temperature (Table 2). The strongest effect was that of PCGA (note the large standardized regression coefficient), fol-

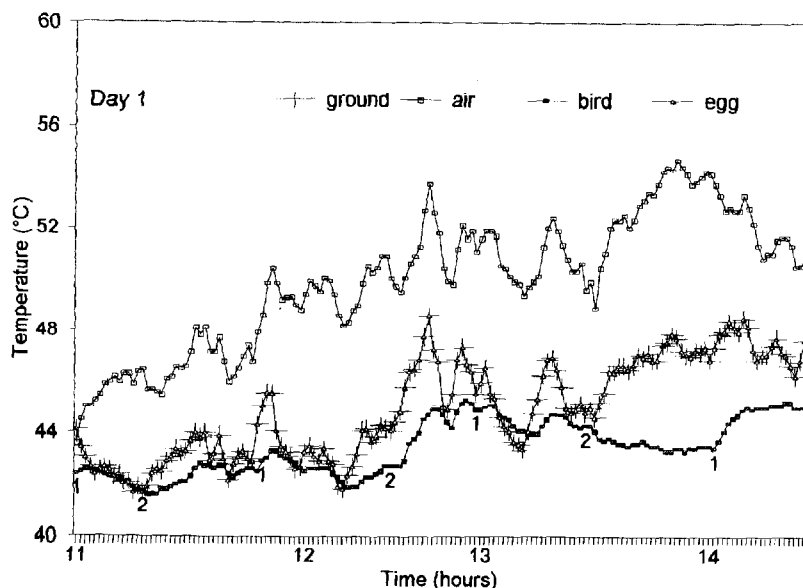


FIG. 3. Model plover body temperature when raised and lowered alternately off the model egg every 30 min (1 = bird on egg, 2 = bird shading egg), showing change in egg temperature, together with air temperature and ground temperature, during experiment 3.

lowed by bird temperature. Bird position had a weak (but significant) effect on egg temperature, and wind speed had no significant effect on egg temperature (Table 2).

In contrast, bird temperature was significantly affected by bird position (ANCOVA with PCGA and wind speed as covariates;  $F = 5.1$ ,  $df = 1$  and  $482$ ,  $P = 0.024$ ). The mean adjusted bird temperature was  $36.76 \pm 0.08^\circ\text{C}$  ( $n = 256$ ) when the bird was on the egg and  $36.50 \pm 0.08^\circ\text{C}$  ( $n = 230$ ) when the bird was shading the egg. Thus, on average, the model bird temperature was lowered by  $0.3^\circ\text{C}$  during shading behavior.

A multiple regression analysis with bird temperature as the dependent variable and

wind speed, bird position (on or above the egg), and PCGA as the independent variables showed that there was a significant overall effect of these variables on bird temperature ( $F = 2177.430$ ,  $df = 1$  and  $482$ ,  $P < 0.0005$ ). All three independent variables had a significant effect on egg temperature (Table 3). The strongest effect was that of PCGA. Wind speed and bird position had weak (but significant) effects on bird temperature (Table 3).

#### DISCUSSION

Several studies have shown the importance of shading to reduce body temperature in desert organisms. For example, Cape ground squirrels (*Xerus inauris*; Bennett et al. 1984) and

TABLE 2. Multiple regression results when egg temperature was plotted against bird position, bird temperature, PCGA,<sup>a</sup> and wind speed.

Independent variable	Standardized coefficient	<i>t</i>	<i>P</i>
Bird position	0.019	2.4	0.017
Bird temperature	0.405	14.0	<0.0005
PCGA	0.593	20.0	<0.0005
Wind speed	0.010	1.2	0.224

<sup>a</sup> First principal component of air and ground temperature.

TABLE 3. Multiple regression results when temperature of the bird was plotted against bird position, wind speed, and PCGA.<sup>a</sup>

Independent variable	Standardized coefficient	<i>t</i>	<i>P</i>
Bird position	-0.027	2.3	0.024
Wind speed	-0.073	6.0	<0.0005
PCGA	0.947	78.0	<0.0005

<sup>a</sup> First principal component of air and ground temperature.

antelope ground squirrels (*Ammospermophilus leucurus*; Chappell and Bartholomew 1981) shade themselves with their tails to reduce body-temperature increments. More frequently, however, animals use objects to shade themselves and lower their body temperature. The most obvious way in which birds shade their eggs is by building a nest under the canopy of a plant. Maximizing radiant cover of the nest reduces heat stress (Walsberg and King 1978), although the degree of radiant cover may be dependent on nest placement (With and Webb 1993). However, shorebirds nesting on the ground in hot environments frequently have no access to shade. Their penchant for nesting in the middle of open areas probably is related to the need for unrestricted views of potential predators in the exposed habitats they occupy (Ward 1990). This habitat choice places severe physiological stress on shorebirds, particularly because air temperatures frequently exceed body temperatures in the heat of the day, resulting in a net heat gain (Grant 1982, Ward 1990).

In our study, an unshaded model of a Crowned Plover egg exposed on a shale substrate gained heat so that it was just 2.5°C lower than ambient air temperature. However, when the egg was loosely covered by the Crowned Plover model, egg temperature was 10°C lower than air temperature. These results indicate that incubation serves to lower egg temperatures significantly, even during the heat of the day.

The experiment in which we raised and lowered the bird model to simulate shading behavior showed that bird position had a significant effect on egg temperature. However, after removing the effects of PCGA and wind speed, we found no significant effect of bird position. In contrast, bird temperature was significantly lower during shading behavior, even after the effects of the above-mentioned environmental variables were removed. Therefore, our data support hypothesis 2 and contradict hypothesis 1. That is, shading behavior serves to cool the incubating bird when it is raised out of the boundary layer and therefore only indirectly cools the eggs (vs. direct cooling by convection). The role of convective cooling of the bird versus the egg is further indicated by the significant negative effect of wind speed on bird temperature but not egg temperature (Tables 2

and 3). Both hypotheses suggest that shading behavior evolved to cool the eggs, but they differ in that the first hypothesis assumes that the eggs are cooled directly, whereas the second assumes that the eggs are cooled as a result of the lowering of the incubating bird's body temperature. We note that the behavior dictated by the second hypothesis could have evolved purely for the direct benefits to the incubating adults, even if this behavior does not lower egg temperature. We infer that a consequence of this behavior is that the eggs subsequently would be cooled.

Little is known about lethal body temperatures in the genus *Vanellus*. An upper limit of 39°C has been suggested by Webb (1987). If this value is pertinent for Crowned Plovers, it would appear that incubating lowered the operative temperature from a potentially lethal level. Further work is necessary to establish how important such reductions in temperature are for egg survival in Crowned Plovers.

Our results indicate the importance of convective cooling of an object that protrudes from the boundary layer. The incubating bird projects itself out of the boundary layer, particularly when it is raised on its tibiotarsi during shading. Wind speed typically increases exponentially with increasing distance from the ground surface (see Campbell 1977, Gates 1980, Goodfriend et al. 1991). Thus, the bird is able to take advantage of convective cooling when it is out of the boundary layer. Furthermore, adult birds may lower their body temperature through shading behavior simply by reducing the degree of contact with the ground surface. Eggs, on the other hand, are positioned in a scrape 1 to 2 cm below ground level. For an egg with a mean maximum diameter of 2.89 cm (Maclean 1993), only 1 to 2 cm projects from the surface of the soil. Thus, most of the egg does not project above the boundary layer for convective cooling to occur.

The potential for convective cooling can be calculated using heat-transfer coefficients for an egg and an adult bird. Following Gates (1980), the heat-transfer coefficient is:

$$h_c = 3.49 \times V^{0.5} \times D^{-0.5}, \quad (2)$$

where  $V$  is wind velocity ( $\text{m s}^{-1}$ ) and  $D$  is the characteristic dimension (m) of the object (i.e. the diameter of the object facing into the wind). We assumed that the egg and the bird were ef-

fectively spherical (see Mitchell 1976). We used the mean maximum diameter of the egg (i.e. 2.89 cm) and a body diameter of 10 cm as the characteristic dimensions. From this equation, we calculated the best-fit regression for  $h_c$  of the egg and the bird against wind speed. For the bird,  $h_c = 0.349(\text{wind speed})$ , and for the egg,  $h_c = 0.1009(\text{wind speed})$ . Thereafter, we estimated wind speed at mid-height for the egg and the bird using equations in Campbell (1977: 38–40) and calculated  $h_c$  at mid-height for the egg and the bird from above the regression equations. When the bird is sitting on the eggs,  $h_c = 0.82 \text{ m}^2 \text{ s}^{-1}$ , whereas  $h_c = 0.91 \text{ m}^2 \text{ s}^{-1}$  when the bird is raised 2 cm on its tibiotarsi during shading. Thus, the bird may effect an 11% increase in the rate of heat transfer by raising its body out of the boundary layer. In contrast,  $h_c$  for the egg is  $0.14 \text{ m}^2 \text{ s}^{-1}$ , or 5.9 times smaller than that of the bird during incubating. This value was calculated assuming the egg was on a flat surface, rather than in a nest scrape. If we assume that only 1 cm of the egg projects above the ground surface,  $h_c = 0.08 \text{ m}^2 \text{ s}^{-1}$ . Thus, the egg has a very low convective heat-transfer coefficient and is unlikely to lose heat from shading behavior.

In conclusion, we consider shading behavior of incubating shorebirds in hot environments to have evolved to facilitate cooling of the incubating bird rather than cooling of the egg. Strictly speaking, therefore, this is not shading behavior but rather convective cooling behavior on the part of the adult.

#### ACKNOWLEDGMENTS

We thank Tamar Cassidy of the Transvaal Museum for the Crowned Plover used to make the model, and Craig Symes and Lynne Broomhall for assisting with the experiments. We are grateful to Amos Ar for suggesting hypothesis 2, and to him, Ralph Ackerman, and Berry Pinshow for discussions of these issues. We thank Berry Pinshow and Gordon Maclean for commenting on an earlier draft of the manuscript. We are grateful to the late Olaf Wirminghaus for making the plover model and discussing ideas. This is publication number 237 of the Mitrani Center for Desert Ecology and publication number 65 of the Ramon Science Center. We dedicate this paper to the memory of Olaf Wirminghaus: husband, friend, and natural historian extraordinaire.

#### LITERATURE CITED

- AR, A., C. V. PAGANELLI, R. B. REEVES, D. G. GREENE, AND H. RAHN. 1974. The avian egg: Water vapor

conductance, shell thickness and functional pore area. *Condor* 76:153–158.

- ARAD, Z., I. GAVRIELLI-LEVIN, AND J. MARDER. 1988. Adaptation of the pigeon egg to incubation in dry, hot environments. *Physiological Zoology* 61:293–300.
- BAKKEN, G. S. 1976. A heat-transfer analysis of animals: Unifying concepts and the application of the metabolism chamber data to field ecology. *Journal of Theoretical Biology* 60:337–384.
- BAKKEN, G. S. 1980. The use of the standard operative temperature in the study of the thermal energetics of birds. *Physiological Zoology* 53:108–119.
- BENNETT, A. F., R. B. HUFY, J. A. HENRY, AND K. A. NAGY. 1984. The parasol tail and thermoregulatory behavior of the Cape ground squirrel, *Xerus inauris*. *Physiological Zoology* 57:57–62.
- CAMPBELL, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, Berlin.
- CHAPPELL, M. A., AND G. A. BARTHOLOMEW. 1981. Standard operative temperature and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. *Physiological Zoology* 54:81–93.
- GATES, D. M. 1980. Biophysical ecology. Springer-Verlag, New York.
- GOODFRIEND, W., D. WARD, AND A. SUBACH. 1991. Standard operative temperatures of two desert rodents, *Gerbillus allenbyi* and *Gerbillus pyramidum*: Microhabitat and environmental factors. *Journal of Thermal Biology* 16:157–166.
- GRANT, G. S. 1982. Avian incubation: Egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithological Monographs* No. 30.
- HENDERSON, S. M. 1963. On-the-farm egg processing, part 3: Thermal conductivity, generalized cooling procedure and cooling in water. *Transactions of the American Society of Agricultural Engineers* 6:95–97.
- HOWELL, T. R. 1979. Breeding biology of the Egyptian Plover, *Pluvianus aegyptius*. University of California Press, Berkeley.
- JAYAKAR, S. D., AND H. SPURWAY. 1965. The Yellow-wattled Lapwing, *Vanellus malabaricus* (Boddaert), a tropical dry-season nester. II. Additional data on breeding biology. *Journal of the Bombay Natural History Society* 62:1–14.
- KILGORE, D. L., D. F. BOGGS, AND G. F. BIRCHARD. 1979. Role of rete mirabile ophthalmicum in maintaining the body-to-brain temperature difference in pigeons. *Journal of Comparative Physiology* 129:119–122.
- MACLEAN, G. L. 1967. The breeding biology of the Double-banded Courser *Rhinoptilus africanus* (Temminck). *Ibis* 109:556–559.
- MACLEAN, G. L. 1972. Egg-covering in the Charadrii. *Ostrich* 45:167–174.

- MACLEAN, G. L. 1975. Belly-soaking in the Charadriiformes. *Journal of the Bombay Natural History Society* 72:74-82.
- MACLEAN, G. L. 1976. A field study of the Australian Pratincole. *Emu* 76:171-182.
- MACLEAN, G. L. 1993. Roberts' birds of southern Africa, 6th ed. John Voelcker Bird Book Fund, Cape Town, South Africa.
- MITCHELL, J. W. 1976. Heat transfer from spheres and other animal forms. *Biophysics Journal* 16: 561-569.
- MUNSELL, A. H. 1966. *Munsell book of color*. Kollmorgen Corporation, Baltimore, Maryland.
- PINSHOW, B., M. H. BERNSTEIN, C. E. LOPEZ, AND S. KLEINHAUS. 1982. Regulation of brain temperature in pigeons: Effects of corneal convection. *American Journal of Physiology* 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.
- SCHMIDT-NIELSEN, K. 1965. Desert animals: Physiological problems of heat and water. Clarendon Press, Oxford.
- VLECK, C. M. 1981. Hummingbird incubation: Female attentiveness and egg temperature. *Oecologia* 51:199-205.
- VLECK, C. M., D. F. HOYT, AND D. VLECK. 1979. Metabolism of avian embryos: Patterns in altricial and precocial birds. *Physiological Zoology* 52: 363-377.
- WALSBERG, G. E., AND J. R. KING. 1978. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. *Physiological Zoology* 51:92-103.
- WALSBERG, G. E., AND W. W. WEATHERS. 1986. A simple technique for estimating operative environmental temperature. *Journal of Thermal Biology* 11:67-72.
- WARD, D. 1987. The biology and systematic relationships of Crowned, Black-winged and Lesser Black-winged Plovers. Ph.D. thesis, University of Natal, Pietermaritzburg, South Africa.
- WARD, D. 1988. Belly-soaking in the Blacksmith Plover *Vanellus armatus*. *Ostrich* 59:142.
- WARD, D. 1989a. Allometry and the breeding biology of some plovers. Pages 371-384 in *Perspectives in vertebrate science*, vol. 5. Alternative life-history styles of animals (M. Bruton, Ed.). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- WARD, D. 1989b. Behaviours associated with breeding in Crowned, Black-winged and Lesser Black-winged plovers. *Ostrich* 60:141-150.
- WARD, D. 1990. Incubation temperatures and associated behavior of Crowned, Black-winged, and Lesser Black-winged plovers. *Auk* 107:10-17.
- WARD, D., AND MACLEAN, G. L. 1989. Habitat selection of Crowned, Black-winged and Lesser Black-winged plovers. *Ostrich* 60:49-54.
- WARD, D., AND B. PINSHOW. 1995. Thermoregulation of desert-dwelling Great Grey Shrikes *Lanius excubitor*. II. Field measurements of standard operative temperatures and relationships with time-activity budgets. *Journal Thermal Biology* 20:271-279.
- WEAST, R. C. (Ed.). 1986. *CRC handbook of chemistry and physics*. CRC Press, Boca Raton, Florida.
- WEBB, D. R. 1987. Thermal tolerance of avian embryos: A review. *Condor* 89:874-898.
- WHITTOW, G. C. 1986. Regulation of body temperature. Pages 221-252 in *Avian physiology* (P. D. Sturkie, Ed.). Springer-Verlag, New York.
- WITH, K. A., AND D. R. WEBB. 1993. Microclimate of ground nests: The relative importance of radiative cover and wind breaks for three grassland species. *Condor* 95:401-413.

Associate Editor: M. E. Murphy