The Condor 89:863–868

VENTILATED CAPSULE MEASUREMENTS OF CUTANEOUS EVAPORATION IN MOURNING DOVES[1]

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Abstract. To determine the contribution of cutaneous water loss to evaporative cooling in Mourning Doves (*Zenaida macroura*), we used a ventilated capsule technique to measure evaporation from the breast, back, and axilla of captive doves at 25 and 35°C. Water loss from these surfaces averaged 4.1 ± 0.4 mg m^{-2} sec^{-1} (SE) at 25°C and was highest from the dorsum. At 35°C, cutaneous evaporation increased to 8.3 ± 0.9 mg m^{-2} sec^{-1}. Mean skin water-vapor diffusion resistance of the breast, back, and axilla together was 111.5 ± 9.5 sec/cm at 25°C and decreased significantly to 69 ± 8.0 sec/cm at 35°C. The large increases in cutaneous evaporation we observed between 25 and 35°C result mainly from temperature-dependent reductions in the skin resistance to water loss. Our results suggest that augmented cutaneous evaporation is utilized as a means of heat defense by Mourning Doves.

Key words: Columbiformes; evaporative water loss; integument; thermoregulation; Zenaida macroura.

INTRODUCTION

Water lost by evaporation from the skin has been recently found to contribute significantly to evaporative cooling responses of columbiform birds to heat stress (Marder and Ben-Asher 1983, Webster et al. 1985). Many previous analyses of avian thermoregulatory physiology had assumed that cutaneous evaporative water loss was negligible in comparison to panting and gular flutter as a means of regulating hyperthermia. However, evaporation from the skin is now known to be about 40 to 75% of total evaporative water loss in most avian species so far studied. Cutaneous water loss has been measured from the whole body using partitioned chambers (Smith 1969, Bernstein 1971, van Kampen 1971, Appleyard 1979, Webster et al. 1985) and from small sections of the skin with desiccant-containing capsules (Hattingh 1972, Withers 1983) or using a leaf diffusion porometer (Marder and Ben-Asher 1983). For this study, we developed and tested a ventilated capsule technique for water loss measurement similar to apparatus used for the measurement of mammalian sweat rates (McLean 1963, Brengelmann et al. 1975).

Mourning Doves, *Zenaida macroura,* are mid-sized (120 g) columbiform birds occurring commonly throughout most of North America. Populations residing in the arid southwestern U.S. deserts inhabit very hot, dry environments and often breed successfully during periods when daytime air temperatures exceed 45°C (Bartholomew and Dawson 1954, Walsberg and Voss-Roberts 1983). To investigate the possibility that the heat tolerance of Mourning Doves is related to an exceptional cutaneous evaporative cooling ability similar to that of other columbiforms (Marder and Ben-Asher 1983), we measured water loss from the skin and estimated the cutaneous water-vapor diffusion resistance (Webster et al. 1985) of three body regions at thermally neutral and high air temperatures.

METHODS

The apparatus for the measurement of cutaneous evaporative water loss consisted of a Teflon capsule ventilated with a positive-pressure airstream and applied to an animal's surface. We pumped air into the capsule via an open flow system (Fig. 1) in which a portion of the flow passed first through a column of desiccant (Drierite), then through a Gilmont (#2) rotameter. We adjusted the humidity of the capsule's inlet air by regulating the fraction of the air that was dried. Air flowed into the capsule at 0.75 to 0.85 l/min (STPD), then out through a second rotameter and into a glass chamber containing the sensor of a humidity meter (Weathertronics 5118). This instrument measures relative humidity to ±0.1%, and was accurate to ±1% RH at 20°C. Inlet air

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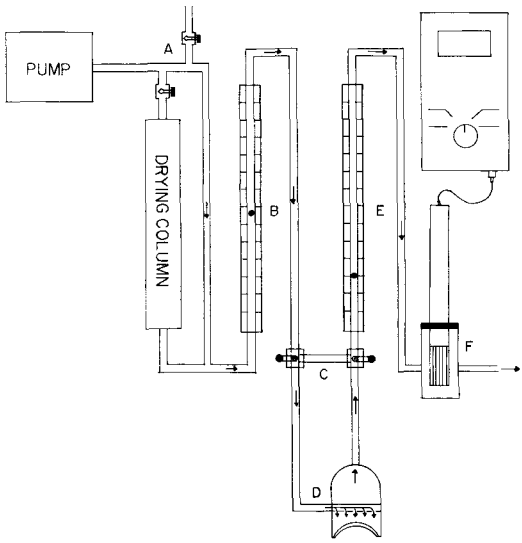

FIGURE 1. The ventilated capsule apparatus used in our measurements. We achieved a predetermined humidity level (RH = 10 to 20%) in the inlet air stream by mixing ambient air with air that had passed through a column of Drierite. Needle valves (A) were used to adjust inlet flow rate and the fraction of inlet air that was dried. We monitored inlet and outlet flow rate using calibrated rotameters (B) and (E). We measured cutaneous evaporation rate by placing the Teflon capsule (D) against the bird's plumage so that outlet air passed through rotameter (E) and across the humidity sensor (F). Inlet air humidity was checked before and after each measurement by switching three-way valves (C) to bypass the capsule. Water loss was computed as the product of inlet flow rate and the difference between incurrent and excurrent water vapor density.

humidity was measured by directing air through tubing that bypassed the capsule.

The capsule was hand-shaped from a 30-ml Teflon TFE centrifuge tube to fit the contours of a dove's body. Its volume after modification was 19.4 ml, and the area of skin covered by the capsule was 6.4 cm^2. Air was forced into the capsule at one side and through small holes in a manifold of Teflon tubing passing through the capsule and glued (Duro Cement Filler) to the other wall. Effluent air left the capsule through an opening in the rounded top. Prior to gluing, Teflon parts were pre-treated with Tetra-Etch (W. L. Gore Associates).

The humidity sensor and meter were calibrated weekly over saturated solutions of LiCl and K_2SO_4. We checked the accuracy of the humidity sensor at nine levels of RH within the range used for our experiments (10 to 25% RH at 25°C) by comparing dew points calculated from relative humidity determinations with those measured by a dew-point hygrometer (EG&G 992) accurate to ±0.25°C. Previously, we had calibrated the hygrometer by substituting precision resistors for the instrument's thermistor. Dew point temperatures computed from RH values obtained with the humidity sensor agreed with the hygrometer to within ±0.15°C.

We calibrated our rotameters with a Brooks Vol-U-Meter (model 1058) using dry air. Repeated flow measurements in the range that we used varied by less than 2%. We computed the range of possible error in our system as the product of potential error in flow and humidity measurements as applied to Equation 1 (below). Typical errors in evaporation rate probably did not exceed ±10% at 25°C and ±5% at 35°C. Errors in individual measurements may be as high as twice these values.

EXPERIMENTAL PROCEDURE

Eight adult Mourning Doves (body mass 109.4 ± 1.1 g [SE]), three male and five female, were live-trapped in Dona Ana County, New Mexico. For 2 weeks prior to our experiments, we housed the birds in individual 0.3-m^3 cages at 25°C and 40 to 50% RH on a 12:12 light-dark cycle. They were allowed free access to millet, pigeon feed (Purina), and water. For our 35°C experiments, we allowed 1 week for acclimation to the new air temperature before collecting data.

We measured cutaneous evaporation rate at 25 and 35°C in a walk-in environmental chamber maintained within ±0.5°C of the selected temperature. To minimize artifacts caused by restraint-induced struggling, these indoor measurements were made in dim light and with a black cloth hood over the dove's head. Similar measurements were made in an outdoor aviary on the same birds after 1 week of acclimatization to natural photoperiods and temperatures. These outdoor measurements took place at air temperatures near 35°C and were made in a shaded enclosure protected from the wind.

We measured water loss from feathered regions of the anterior breast, from the axilla, and from the cranial portion of the back. We did not seal the capsule to the skin, but held it in place so that a portion (50 to 75%) of the inlet flow passed through the outlet rotameter and to the humidity sensor. This method assumes that humidified air leaking from under the edges of

the capsule is of the same composition (humidity) as air in the capsule efflux line.

Fine copper-constantan thermocouples embedded in 22 ga. hypodermic needles were used to measure subcutaneous skin temperature near the site of capsule placement. Temperatures were recorded from a Bailey Bat-12 thermocouple reader calibrated by a mercury thermometer with accuracy (±0.1°C) traceable to the U.S. National Bureau of Standards.

All measurements were taken within 5 min of first capturing the bird from its cage and hooding it. Each individual determination of evaporation rate involved checking inlet humidity, positioning the capsule, and recording steady-state RH from the humidity meter. We measured evaporation from all three body regions, in random order, on each dove at least once at each indoor air temperature. At least 24 hr passed between successive measurements on an individual bird. Airflow rates and effective volume of the system were such that steady readings were obtained within 1 to 1.5 min of capsule placement. During this time skin temperatures rarely climbed more than 0.2°C, indicating that we obtained our data before excitement-caused hyperthermia could affect our measurements.

ANALYSIS

We computed the density of water vapor in capsule inlet and outlet air from RH and temperature measurements using Tetens' equations from Bernstein et al. (1977). Water loss rates were calculated using the expression:

$$\dot{E}_c = \dot{V}_{in}(\rho_{Vout} - \rho_{Vin})/A_c \qquad (1)$$

where $\dot{E}_c$ is evaporation rate in g m^{-2} sec^{-1}, $\dot{V}_{in}$ is inlet flow rate in m^3 sec^{-1}, ρ_v is water vapor density in gm^{-3}, and A_c is capsule cross-sectional surface area (6.4×10^{-4} m^2).

The tissue beneath the skin was assumed to be saturated with water vapor at subcutaneous skin temperature, allowing the resistance to water vapor loss of the integument beneath the capsule to be calculated by the formula:

$$r_v = 0.01[(\rho'_{vs} - \rho_{va})/\dot{E}_c], \qquad (2)$$

where r_v is the sum of tissue, plumage, and boundary-layer resistance to water vapor diffusion (sec/cm), and ρ'_{vs} and ρ_{va} are the water vapor densities (g/m^3) beneath the skin and in the air above the plumage, respectively. The water vapor density in the capsule was assumed not to be significantly different from that in the inlet air, because flow rate was high in comparison to evaporation rate. Since the plumage and boundary layer contribute a relatively small fraction of the water-vapor diffusion resistance (Campbell 1977, Webster et al. 1985), we shall henceforth refer to the water-vapor transport coefficient as the skin resistance (r_{vs}).

The latent heat of vaporization of water was taken as 2,450 J/g for calculations of latent heat loss. To compute metabolic heat production from literature values for Mourning Dove oxygen consumption, we used 20.1 J/cm^3 as the caloric equivalent for oxygen. We estimated surface areas of the doves by geometric approximation and by using the Meeh equation as modified by Walsberg and King (1978).

We compared the results of measurements made under different conditions and from different body regions by an analysis-of-variance model incorporating unequal replicates. We examined the data for significant differences using the least-significant-difference test. Student *t*-tests were used to compare indoor and outdoor measurements. For each test, we accepted the hypothesis that the means differed when the probability of error was less than 5%. All data are presented as means ± SE.

RESULTS

Measurements of $\dot{E}_c$ and subcutaneous temperature and calculated values of r_{vs} in doves at 25 and 35°C are presented in Table 1. Inlet air humidity was higher at 25°C (4.5 ± 0.2 g/m^3) than at 35°C (2.9 ± 0.02 g/m^3), so water loss rates at these two temperatures are not strictly comparable with each other. However, we corrected these measurements for inlet ρ_{va} using the water-vapor diffusion resistance model of Webster et al. (1985) and found that $\dot{E}_c$ in all regions increased significantly between 25 and 35°C. Furthermore, evaporation was significantly slower from axillary skin at 25°C and significantly faster from the back at 35°C than from the other skin regions. At 35°C, resistance to water loss (r_{vs}) was significantly lower in the back than in breast and axillary skin, whereas at 25°C, r_{vs} was higher in the axilla than elsewhere. Between 25 and 35°C, r_{vs} decreased significantly in all body regions.

In the outdoor aviary, water loss rates were more variable but were similar to indoor measurements. We collected data on seven birds when the air temperature was 35.8 ± 0.4°C and air

TABLE 1. Cutaneous evaporation, subcutaneous skin temperature, and water-vapor diffusion resistance of Mourning Doves (*Zenaida macroura*) at 25 and 35°C. Measurements were made on eight birds of mean body mass 109.4 ± 1.1 g. All values are means ± SE.

Body region	Number of replicates	Evaporation rate (mg m^{-2} sec^{-1})	Subcutaneous temperature (°C)	Vapor diffusion resistance (sec/cm)
Air temperature 25°C				
Breast	23	4.12 ± 0.30	40.0 ± 0.13	110.5 ± 8.2
Back	18	4.86 ± 0.53	38.9 ± 0.27*	90.8 ± 10.8
Axilla	22	3.48 ± 0.29*	40.5 ± 0.20	133.4 ± 9.5*
Air temperature 35°C**				
Breast	13	6.81 ± 0.55	42.1 ± 0.16	75.7 ± 8.5
Back	14	11.93 ± 1.40*	41.2 ± 0.16*	44.2 ± 4.8*
Axilla	14	6.28 ± 0.72	42.2 ± 0.22	86.8 ± 10.6

* Values differ significantly ($P < 0.05$) from others at this temperature.
** For all body regions, evaporation rate and skin temperature were significantly higher, and vapor resistance significantly lower, at 35°C than at 25°C ($P < 0.05$).

humidity was 5.5 to 6.1 g/m^3 inside the aviary. Capsule inlet air humidity (4.3 ± 0.1 g/m^3) was similar to that used in our indoor 25°C experiments. No significant differences in $\dot{E}_c$, subcutaneous temperature, or r_{vs} between body regions were present in these measurements, so we pooled the data. Subcutaneous skin temperature was 41.2 ± 0.2°C, similar to that measured indoors at 35°C. Average cutaneous evaporation rate was 7.17 ± 0.82 mg m^{-2} sec^{-1}, and the skin resistance to water loss was 74.6 ± 7.6 sec/cm. When corrected for differences in inlet air humidity as before, none of these data differ significantly from comparable data collected indoors at 35°C.

DISCUSSION

Our estimates of cutaneous evaporation rate in Mourning Doves at 25°C are lower (by 10 to 40%) than those of Marder and Ben-Asher (1983) for the Palm Dove (*Streptopelia senegalensis*), Collared Turtle-Dove (*S. decaocto*), and Rock Dove (*Columba livia*) at 20°C. The cutaneous water loss rates that we measured in Mourning Doves at 35°C were much less (40 to 60% lower) than Marder and Ben-Asher's measurements on other columbids (above) during mild heat stress (36 to 40°C). These differences may reflect real interspecific variation in cutaneous water loss, or may result from dissimilar measurement techniques.

We found that cutaneous evaporation rate, skin temperature and skin water-vapor diffusion resistance all varied regionally over the body surface. This may result from differences in cutaneous vascularization between body surfaces (Wolfenson et al. 1981) or regional variation in epidermal lipid deposition (Lucas 1980). Alternatively, the thickness of the stratum corneum may vary over the body surface and thus provide a less effective barrier to cutaneous water loss in some regions than in others. Further measurements of cutaneous blood flow patterns and epidermal histology of birds are needed to explain regional variations in cutaneous evaporation such as those we observed.

To estimate the contribution of cutaneous evaporation to the heat and water budgets of free-living doves, we calculated daily rates of skin water loss based on our measurements. We computed a mean whole-body water-vapor diffusion resistance for Mourning Doves based on weighted contributions of the back, breast, axilla, and feet. We estimated the relative proportions of surface area using geometric approximation techniques, and used the following values: back, 28%; breast, 28%; axilla, 14%; wings, 14%; head and neck, 10%; feet and legs, 6%. We assumed that the skin of the wings, head, and neck had r_{vs} similar to the average of the three body surfaces from which we measured water loss. Since the scaled legs and feet are much less water-permeable than the rest of the body (M. H. Bernstein, unpubl. data), we assumed that r_{vs} for these surfaces was 600 sec/cm, similar to the skin resistance of reptiles (Campbell 1977). We estimate that average skin resistance to water loss in doves is 138 sec/cm at 25°C and 98 sec/cm at 35°C. At a mean air temperature of 25°C, air humidity of 6.6 g/m^3 (obtained from meteorological data for Las Cruces, New Mexico in July 1985) and an assumed mean skin temperature of 40°C, we estimate that cutaneous evaporation is 4.4 g/day in a 109-g dove. This is equivalent

to the loss of 4.0% of body weight per day, or 40% of the ad libitum water intake of caged birds (9.9% of body mass per day, Bartholomew and MacMillen 1960). These calculations, based on conservative estimates of the gradient for water vapor diffusion through the skin, demonstrate that cutaneous evaporation is an important component of the daily water budgets of Mourning Doves.

We estimate that latent heat loss resulting from cutaneous evaporation in doves is 6.4 W per m^2 of external (plumage) surface area at 25°C. At 35°C, the corresponding figure calculated from our data is 10.7 W/m^2. The basal metabolic rate of Mourning Doves reported by Hudson and Brush (1964) is 41.7 W/m^2. On the basis of our results, we calculate that cutaneous evaporation in nonheat-stressed doves accounts for the dissipation of 15 to 24% of basal metabolic heat production, and that at 35°C water loss from the skin dissipates from 26 to 49% of metabolic heat in resting birds. Cutaneous evaporative cooling thus may also be a significant avenue for heat defense in doves.

Skin water-vapor diffusion resistance in Mourning Doves and other columbiforms apparently declines significantly from thermoneutral levels when air temperature is high. Appleyard (1979), working with Ringed Turtle-Doves (*Streptopelia risoria*), first suggested that such changes in the water permeability of avian skin might contribute to evaporative cooling in birds. In support of this hypothesis, Webster et al. (1985) measured sharp declines in whole-body water-vapor diffusion resistance in pigeons and calculated reduced resistance to cutaneous water loss during heat stress in several additional avian species. This phenomenon may result from increased cutaneous bloodflow, from steric changes in epidermal lipids, or from increased hydration of the keratin layer of the stratum corneum (Webster et al. 1985). At present, we possess no information to explain the observed changes in skin water permeability. Our results, however, lend further support to Marder and Ben-Asher's (1983) suggestion that pigeons and doves may possess a greater capacity for cooling by cutaneous evaporation than other birds.

ACKNOWLEDGMENTS

This study was supported by a grant from the National Science Foundation (DCB-8118956) to MHB. We thank Sanford Schemnitz and Gary Cunningham for the loan of equipment and Dennis Hudson, Shawn Pierce, and Berry Pinshow for assistance and helpful discussions which improved the study. Ken Kunkel, New Mexico Department of Agriculture Climatologist, kindly provided us with meterological data for the Las Cruces area.

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