

TEMPERATURE REGULATION IN TURKEY VULTURES¹

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Abstract. Temperature regulation by six Turkey Vultures (*Cathartes aura*) was studied at ambient temperatures (T_a) from 11 to 40°C in a metabolic chamber. Within this range body temperature varied little, averaging 39.7°C, and the ratio of CO₂ production to O₂ consumption averaged 0.76. The thermal-neutral zone (TNZ) extended from 26 to 40°C. Below 26°C evaporative water loss and the heat-transfer coefficient were minimal, reflecting maximum insulation, and breathing and heart rates remained nearly constant at 10 and 142 min⁻¹, respectively. Oxygen consumption increased by 12 μ l O₂ STPD/(g hr) per °C of decrease in T_a below 26°C, so the percentage of metabolic heat lost by evaporation decreased from 22 to 13%.

Within the TNZ O₂ consumption was minimal, averaging 0.73 ml STPD/(g hr), but evaporation increased exponentially, dissipating metabolic heat to a maximum of about 90% at 40°C. Insulation decreased exponentially within the TNZ. Despite this, however, the birds underwent rapid hyperthermia above 40°C. The likely explanation for this is that under the present experimental conditions the Turkey Vultures could not make use of important behavioral components of their thermoregulatory repertoire, including neck extension, wing spreading, and urination on the legs. Were this not so they likely would have exhibited greater reduction in insulation and tolerated higher T_a . The thermal relations of Turkey Vultures were similar to those calculated from allometric relations and to those measured previously in the closely related, partially sympatric Black Vulture (*Coragyps atratus*).

Key words: *Cathartes aura*; evaporative water loss; Falconiformes; heat loss; metabolism; oxygen consumption; temperature regulation; Turkey Vulture.

INTRODUCTION

New-World vultures use novel means to increase heat loss during heat exposure. They extend the bare skin of the neck and head, spread the wings, and urinate on their legs (urohidrosis). Temperature regulation has been comprehensively studied in Black Vultures (*Coragyps atratus*) both during heat exposure at rest (Enger 1957, Larochelle et al. 1982), and during exercise (Mahoney 1983). Only fragmentary data on temperature regulation are available for the partially sympatric Turkey Vultures (*Cathartes aura*) (Enger 1957, Heath 1962, Hatch 1970). We therefore undertook this study to provide a more complete account of the Turkey Vulture's thermal relations at rest for comparison with Black Vultures and other falconiforms.

MATERIALS AND METHODS

We used six Turkey Vultures having a body mass that ranged from 1,256.9 to 1,526.4 g with a

mean of 1,380.3 \pm 106.8 g (SD). After capture in southern Arizona, they were transported to New Mexico State University and kept in an outdoor aviary (6 m \times 6 m \times 4 m tall) partly covered for shade and shielded against wind. Heat was supplied by two 250-W infrared lamps during winter. Commercial bird-of-prey diet and water were supplied ad libitum.

All experiments were performed during the months of January through May. Before each experiment a bird was deprived of food and water for at least 24 hr and weighed to the nearest 0.1 g. A copper-constantan thermocouple (outside diameter 0.7 mm), coated with polyethylene tubing (PE 90) to a final diameter of 1.27 mm, was inserted 4 cm into the cloaca to measure body temperature (T_b). The bird was then placed into a 64-liter container that had had its inner walls painted flat black. This was enclosed in an environmental chamber in which the temperature was automatically controlled (\pm 0.5°C). Ambient temperature (T_a) was measured with another thermocouple in the chamber air near the bird. The thermocouples were connected through a

¹ Received 29 April 1988. Final acceptance 2 August 1988.

TABLE 1. Flow rates and resulting water vapor pressures (means \pm SD) in the environmental chamber during experiments on Turkey Vultures carried out within four ranges of ambient temperature (T_a).

T_a °C	Flow rate liter STPD/min	Vapor pressure Torr
10-17	3.40 \pm 0.32	7.53 \pm 1.26
17-32	3.55 \pm 0.52	10.96 \pm 1.92
32-35	4.68 \pm 0.32	13.96 \pm 2.04
35-41	5.41 \pm 0.62	19.41 \pm 3.96

multiplexer (Bailey, model CAL-1) to a digital thermometer (Bailey, model TH-6D), linked in turn to a potentiometric chart recorder (Houston, Omniscrite). All thermocouples and associated recording apparatus were calibrated with a mercury-in-glass thermometer having an accuracy ($\pm 0.1^\circ\text{C}$) traceable to the U.S. National Bureau of Standards (NBS). In a few experiments at ambient temperatures below the zone of thermal neutrality, birds were also instrumented with electrodes connected through an impedance pneumograph and DC amplifier to a two-channel oscillograph (Gould, Brush model 220). Recordings were counted visually to obtain breathing rate (f) and heart rate.

Oxygen consumption (\dot{V}_{O_2}), CO_2 production (\dot{V}_{CO_2}), and evaporative water loss (\dot{m}_e) were measured in an open-flow system. Dry, CO_2 -free air was drawn through the animal chamber by use of a vacuum pump. Evaporation by the bird raised the water vapor pressure of the chamber air, so in accordance with the recommendations of Lasiewski et al. (1966) we used different flow rates through the system at different T_a to regulate vapor pressure below 20 Torr (Table 1).

A sample of chamber outflow air was directed to a dewpoint hygrometer (E G & G, model 992-C1) connected to a digital multimeter (Keithley, model 160). The remainder of the chamber outflow was directed through a column containing a desiccant (Drierite), then through an infrared CO_2 analyzer (Beckman, model 864), and lastly through an oxygen analyzer (Applied Electrochemistry, model S3A). All instrument outputs were recorded on separate potentiometric chart recorders (Houston, Omniscrite).

The accuracy of the hygrometer's output was confirmed by use of a standard resistor with NBS-traceable accuracy (± 0.01 ohm), substituted for the hygrometer's resistance thermometer. The multimeter's accuracy was confirmed by use of

an Eppley standard cell. The O_2 analyzer was calibrated by bypassing the animal chamber in the flow system and maintaining different total system pressures, as determined with a mercury manometer. It was assumed that the O_2 content of system air was 20.95%. The CO_2 analyzer was calibrated by drawing pure CO_2 at known rates into system air from a flow calibrator (Brooks Vol-U-Meter) having NBS-traceable accuracy ($\pm 0.2\%$). System and analyzer flows were measured with Brooks rotameters calibrated by the flow calibrator.

Steady-state values of O_2 , CO_2 , and water-vapor content in the chamber effluent, together with flow rate, were employed to calculate \dot{V}_{O_2} , \dot{V}_{CO_2} , and \dot{m}_e . Gas volumes were corrected to conditions of standard temperature and pressure, dry (STPD). Metabolic rate (heat production, \dot{H}_m) and evaporative heat loss (\dot{H}_e) were calculated from \dot{V}_{O_2} and \dot{m}_e assuming that 1 liter of O_2 consumed is equivalent to 20.09 kJ and that 1 g of H_2O evaporated is equivalent to 2.43 kJ. The heat-transfer coefficient (h) was calculated as $(\dot{H}_m - \dot{H}_e)/(T_b - T_a)$.

Each time a bird was tested it was exposed for 2-3 hr to each of two or three ambient temperatures over the course of one day. Data were used from stable recordings in the last 30 min at each T_a . All experiments were carried out during daylight hours in the alpha phase (Aschoff and Pohl 1970) to avoid diurnal effects. Five birds each were used in 15 experiments and a sixth was used in 12. The data are presented as means \pm standard deviations; where appropriate they have been analyzed by least-squares regression. Presented along with the arithmetic forms of the regression equations are the mean of the independent variable (\bar{T}_a), the standard error of the regression coefficient (S_b), the standard error of the estimate ($S_{y,x}$), and the correlation coefficient (r). Results were considered statistically significant when the probability (P) that the null hypothesis is true was 0.05 or less.

RESULTS

Body temperature did not vary significantly in the T_a range used (10.7-40.4°C), averaging $39.7 \pm 0.6^\circ\text{C}$ for 75 measurements on six vultures. The results of \dot{V}_{O_2} measurements are shown in Figure 1. The lower critical temperature (T_{lc}), above which \dot{V}_{O_2} remained minimal and stable, was determined as recommended by Pinshow et al. (1976), and amounted to 25.6°C. While this

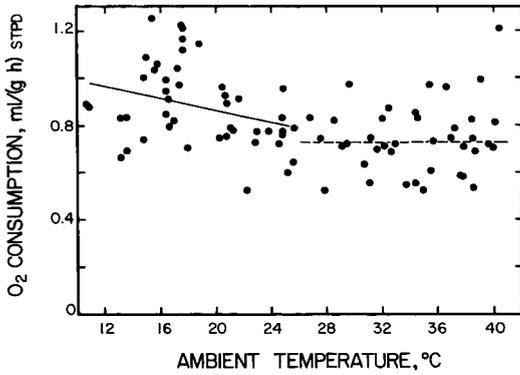


FIGURE 1. Oxygen consumption of Turkey Vultures in relation to ambient temperature. Solid line is the least-squares regression line below the TNZ, as described by equation 1. Dashed line represents mean within the thermal-neutral zone.

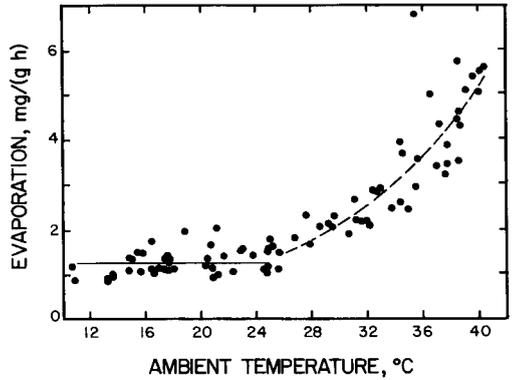


FIGURE 2. Evaporative water loss of Turkey Vultures in relation to ambient temperature. Dashed line is the least-squares regression line described by equation 2, whereas solid line represents mean of data below thermal neutrality.

is the mathematically correct T_{lc} , Figure 1 shows that \dot{V}_{O_2} at T_a between 20.2 and 25.6°C was similar to that above 25.6°C. The TNZ extended to the highest T_a employed, 40.4°C, \dot{V}_{O_2} averaging $0.74 \pm 0.14 \text{ cm}^3/(\text{g hr})$ ($n = 42$). The corresponding mean \dot{H}_m was $5.66 \pm 1.01 \text{ W}$ or $4.14 \pm 0.80 \text{ W/kg}$. Over the full range of T_a below T_{lc} , \dot{V}_{O_2} increased significantly according to:

$$\dot{V}_{O_2} = 1.12 - 0.012T_a, \quad (1)$$

$$\begin{aligned} \bar{T}_a &= 18.7^\circ\text{C}, & S_b &= 0.006, & S_{y,x} &= 0.16, \\ r &= -0.30, & P &= 0.05, & n &= 45. \end{aligned}$$

At 10.7°C, \dot{V}_{O_2} was 0.99 ml/(g hr) (equation 1), 34% higher than the mean within the TNZ. The respiratory exchange ratio ($R = \dot{V}_{CO_2}/\dot{V}_{O_2}$) did not vary significantly with T_a , averaging 0.76 ± 0.04 ($n = 87$), a value within the range reported previously for Black Vultures (0.70–0.83) at T_a of 5 to 42.5°C (Larochelle et al. 1982). Heart and breathing rates below the thermal-neutral zone (TNZ) were invariant. The former averaged $142 \pm 13 \text{ min}^{-1}$ for seven measurements on four of the birds, while the latter averaged $10 \pm 3 \text{ min}^{-1}$ for nine measurements on five birds.

Figure 2 shows that evaporative water loss did not vary significantly below the TNZ, averaging $1.27 \pm 0.29 \text{ mg}/(\text{g hr})$ ($n = 45$). Above the T_{lc} , \dot{m}_e increased significantly with T_a , according to:

$$\dot{m}_e = 0.149e^{0.089 T_a}, \quad (2)$$

$$\begin{aligned} \bar{T}_a &= 34.1^\circ\text{C}, & S_b &= 0.0069, & S_{y,x} &= 0.19, \\ r &= 0.90, & P &< 10^{-14}, & n &= 42 \end{aligned}$$

where e is the base of natural logarithms. At

40.4°C, \dot{m}_e was 5.4 mg/(g hr) (equation 2), more than four times the mean below thermal neutrality. Evaporative water loss below T_{lc} dissipated heat at a mean rate of $1.2 \pm 0.2 \text{ W}$ ($n = 45$). In comparison, \dot{H}_e at T_a of 40.4°C was maximum, amounting to 5.9 W, a nearly five-fold increase. The ratio of \dot{H}_e to \dot{H}_m increased significantly with T_a , but at significantly different rates below and within the TNZ (Fig. 3). The relationship of \dot{H}_e/\dot{H}_m below T_{lc} is:

$$\dot{H}_e/\dot{H}_m = 0.050 + 0.0068T_a, \quad (3a)$$

$$\begin{aligned} \bar{T}_a &= 18.7^\circ\text{C}, & S_b &= 0.0015, & S_{y,x} &= 0.04, \\ r &= 0.58, & P &< 10^{-4} \end{aligned}$$

whereas above T_{lc} the relationship is:

$$\dot{H}_e/\dot{H}_m = 0.030e^{0.083 T_a}, \quad (3b)$$

$$\begin{aligned} \bar{T}_a &= 34.1^\circ\text{C}, & S_b &= 0.0058, & S_{y,x} &= 0.16, \\ r &= 0.91, & P &< 10^{-13}. \end{aligned}$$

Thus evaporation removed between 13 and 22% of metabolic heat below T_{lc} (equation 3a), whereas at T_a of 40.4°C the figure was 86% (equation 3b). This approximately seven-fold increase was caused by both the decrease in \dot{H}_m and by the increase in \dot{H}_e with T_a .

Figure 4 shows that h did not vary significantly below T_{lc} , averaging $0.19 \pm 0.04 \text{ W}/(\text{kg } ^\circ\text{C})$. Within the TNZ, h increased significantly with T_a , according to:

$$h = 0.024 e^{0.0807 T_a}, \quad (4)$$

$$\begin{aligned} \bar{T}_a &= 34.1^\circ\text{C}, & S_b &= 0.012, & S_{y,x} &= 0.28, \\ r &= 0.74, & P &< 10^{-6}. \end{aligned}$$

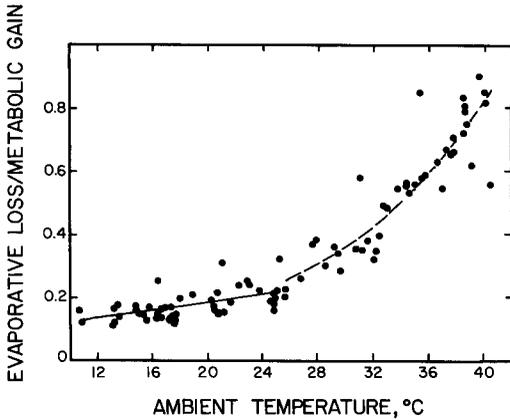


FIGURE 3. Ratio of evaporative heat loss, calculated from m_e data in Figure 2, to metabolic heat production, calculated from $\dot{V}O_2$ data in Figure 1, of Turkey Vultures, as a function of ambient temperature (T_a). Solid line is the least-squares regression line described by equation 3a. Dashed line represents least-squares regression line described by equation 3b.

At T_a of 40.4°C, h was 0.61 W/(kg °C) (equation 4), more than three times the mean below T_{ic} .

DISCUSSION

BODY TEMPERATURE, BREATHING RATE, HEART RATE

The mean T_b of 39.7°C (range = 38.0–41.7°C), measured at T_a between 11 and 40°C, is similar to previously reported T_b values of 38–40°C (Hatch 1970) and 41°C (Enger 1957) for this species. It is also close to values reported for other falconiforms, e.g., 38.9–41.2°C in the Bald Eagle, *Haliaeetus leucocephalus* (Stalmaster and Gessaman 1984); 38.8–39.0°C in the Lammergeier, *Gypaetus barbatus* (Siegfried and Frost 1973); 39.9–41.9°C in the Red-tailed Hawk, *Buteo jamaicensis* (Chaplin et al. 1984); and 39.4–42°C in the Black Vulture (Mahoney 1983). Larochelle et al. (1982) measured extremes of 37.3 and 42.9°C at T_a of 15 and 45°C, respectively, in the Black Vulture. Wasser (1986) has compiled data for 11 falconiform species ranging from 37.1 to 41.3°C and averaging 39.5°C, almost identical to our mean. In contrast to most other studies, we observed no T_b fluctuations during individual experiments and no hypothermia, each bird closely regulating T_b within a narrow range. In addition, there was no indication of the hyperthermia within the TNZ reported for the Black Vulture by Larochelle et al. (1982).

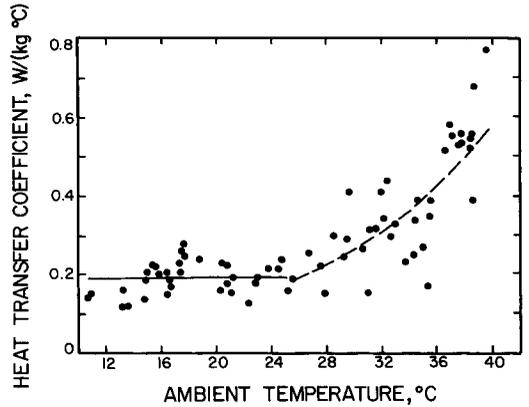


FIGURE 4. Heat-transfer coefficient of Turkey Vultures as a function of ambient temperature. Solid line is the mean of data below thermal neutrality. Dashed line is the least-squares regression line described by equation 4.

Below the TNZ, respiration and heart frequencies did not vary significantly. At 10 min^{-1} , the mean resting f was lower than the rate of 16 min^{-1} calculated allometrically for a 1,380-g nonpasserine bird (Calder 1968), whereas at 142 min^{-1} the mean heart rate was similar to the calculated values of 145 min^{-1} (Calder 1968) and 163 min^{-1} (Grubb 1983).

BEHAVIORAL THERMOREGULATION

Breathing rate was measured below the TNZ only. In a few experiments, however, the birds were visually observed at T_a above the T_{ic} as they stood at rest under dim illumination. Under these conditions, panting was not detected at any T_a below 40°C. In their study on Black Vultures, Larochelle et al. (1982) observed panting at $T_a = 45^\circ\text{C}$, when T_b reached 43°C. We did not expose our vultures to similarly high T_a after two incidents of explosive heat rise during panting at a T_a of 42°C.

After heat-exposed vultures ($T_a > 35^\circ\text{C}$) were returned to the aviary they did not approach food or water despite about 36 hr of deprivation, but immediately perched and assumed a spread-wing posture with the neck extended for 10–15 min. Apparently during heat stress in the chamber the vultures could not avoid hyperthermia because they could not spread their wings nor extend their necks, a response previously documented during heat exposure in this species (Hatch 1970). Larochelle et al. (1982) reported both wing fanning and increased exposure of neck skin in heat-ex-

posed Black Vultures, and this was correlated with higher temperatures in unfeathered skin areas of the beak, legs, and axilla. Wing-spreading by Turkey Vultures may also be important for radiant heat gain on cool mornings (Clark and Ohmart 1985).

Kahl (1963) documented the thermoregulatory role of urinating on the legs in heat-exposed Wood Storks (*Mycteria americana*) and found that urohidrosis plays a major role in this bird's temperature regulation. In the same report, Kahl mentioned urohidrosis in Black Vultures and other New World vultures. Hatch (1970) verified this and found that in heat-exposed Turkey Vultures, as in Wood Storks, leg-wetting contributes substantially to temperature regulation. Kahl reported, however, that restrained storks instrumented for cloacal T_b measurements would not urinate on their legs due to cloacal blockage and the inability to assume the appropriate posture, and this is undoubtedly true for birds confined in a small chamber with a thermocouple in the cloaca. We conclude that Turkey Vultures at rest tolerate T_a greater than 40°C only when able to use important behavioral elements of their thermoregulatory repertoire.

HEAT PRODUCTION

The measured metabolic rate of Turkey Vultures in the TNZ (4.1 W/kg) is 1.4 times the value calculated from Enger (1957). The available data for Black Vultures cover a similar 1.4-fold range: 3.1 W/kg (Larochelle et al. 1982), 3.6 W/kg (Enger 1957), 4.0 W/kg (Grubb 1983), and 4.4 W/kg (Mahoney 1983). In the TNZ of the similar-sized Red-tailed Hawk, Hayes and Gessaman (1979) measured a metabolic rate of 4.2 W/kg, 1.9 times the value obtained by Wasser (1986) in the same species. In the Osprey (*Pandion haliaetus*), Wasser (1986) obtained a value of 3.7 W/kg. Such variations within a species are not unusual and often reflect seasonal, diurnal, sexual, nutritional, and maturational differences, as well as differences in the measurement and handling techniques used. Variations among related species of similar size may be due to these factors as well as to true species differences.

Turkey Vulture heat production within the TNZ in this study was 10% lower and 17% higher, respectively, than calculated by the allometric nonpasserine equations of Grubb (1983) and of Lasiewski and Dawson (1967). The thermal-neutral heat production was, however, identical to

the value calculated by the equation of Aschoff and Pohl (1970) for nonpasserines in alpha phase. Our data were also 59% higher than calculated by the equation of Wasser (1986) for 11 species of falconiforms. Wasser (1986) concluded that members of this group from hot habitats have low metabolic rates compared with species from other habitats. Although found in deserts, Turkey Vultures have a wide North American distribution and are unlikely to have special adaptations for any one habitat. Still, our vultures were winter-acclimatized outdoors, so the possibility that their summer metabolic rates are lower cannot be excluded.

Below thermal neutrality $\dot{V}O_2$ increased (Fig. 1) at the rate of 0.012 ml/(g hr) per °C of decrease in T_a (equation 1), corresponding to an increase in \dot{H}_m of 0.068 W/kg per °C of T_a decrease. This moderate value probably reflects the large size and winter-acclimatized condition of the birds, as well as adjustments that minimize evaporative and possibly convective heat loss. The results are similar to those reported for Black Vultures (Larochelle et al. 1982).

EVAPORATIVE HEAT LOSS

Turkey Vultures minimized evaporative heat loss below thermal neutrality, dissipating 13 to 22% of their metabolic heat production. This is similar to the mean minimum of 25% calculated from the data presented by Mahoney (1983) for the Black Vulture, but higher than the minimum measured by Larochelle et al. (1982) in the same species. Evaporation below TNZ also accords with the value calculated for a 1,380-g bird by the equation of Crawford and Lasiewski (1968).

Within the TNZ the increase in evaporation (Fig. 2) and the stable metabolic rate at T_a up to 40°C (Fig. 1) resulted in the exponential increase in the ratio between evaporative heat loss and heat production shown in Figure 3. The exponent in the expression (equation 3b) that describes this increase is 0.083, a value similar to the exponent of 0.087 calculated by Calder and King (1974) for 20 bird species weighing from 6 g to 100 kg. The highest ratio of evaporative heat loss to heat production we observed in the Turkey Vulture at about 40°C T_a (0.90) is similar to that of Black Vultures at the same T_a but does not necessarily reflect a maximum, since higher T_a s were not employed here. Indeed, Black Vultures dissipated 45% more heat than they produced at 45°C T_a (Larochelle et al. 1982), and it may be that

Turkey Vultures can also attain this level when free to assume appropriate postures.

The data do not permit quantification of the contributions by the respiratory system and skin to the \dot{m}_c increase. Increased respiratory evaporation without increased f has been noted in many species and may be due to increased tidal volume and exhaled-air temperature. Cutaneous evaporation accounts for half or more of total evaporation in several species of birds, especially at elevated T_a (Bernstein 1971, Lasiewski et al. 1971, Marder and Ben-Asher 1983, Webster and King 1987) and may increase with T_a in vultures as well.

HEAT-TRANSFER COEFFICIENT

In the present study the heat-transfer coefficient below T_{lc} averaged 0.19 W/(kg °C). The observed minimum h equals the value calculated by both the equations of Lasiewski (1972) and of Wasser (1986). The minimum value recalculated from Larochelle et al. (1982) and Mahoney (1983) for the Black Vulture, 0.27 and 0.33 W/(kg °C) respectively, are somewhat higher. In Turkey Vultures h increased exponentially with T_a above T_{lc} , and at 40°C was about three times the minimum. This reduction in insulation is undoubtedly due to ptiloerection, increased blood flow in skin, and perhaps wing drooping, and supplements the increase in evaporative heat loss. The maximum value of h in the resting, heat-exposed Black Vulture was about four times (Larochelle et al. 1982), and that of the exercising Black Vulture nearly five times (Mahoney 1983), their respective minimum levels. If neck and wing extension had been possible, our Turkey Vultures at T_a above 40°C might have increased h further.

CONCLUSIONS

The measured thermal responses of Turkey Vultures are similar to values calculated from allometric expressions and roughly agree with those for the closely related and partially sympatric Black Vulture. The Turkey Vulture thrives in a wide range of climates in America (Hatch 1970). The relatively wide TNZ, as well as the moderate increase in metabolic rate and low heat-transfer coefficient during cold exposure, undoubtedly minimize the impact of thermoregulation on cost of living. Thermoregulatory behavior at high ambient temperatures, including neck extension, wing spreading, and urohidrosis, were probably prevented in the present study, thus limiting high-

temperature tolerance in this widely distributed species. Additional study on the importance of these behaviors to the general thermoregulatory strategy of Turkey Vultures remains to be carried out.

ACKNOWLEDGMENTS

We thank Barbara Kimbell for obtaining the vultures, and Lori Harel and Carol Bernstein for typing the manuscript. This study was supported by NSF grant PCM-8118956.

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