THERMOREGULATORY ROLE OF THE UNFEATHERED HEAD AND NECK IN MALE WILD TURKEYS

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ABSTRACT.—The brightly colored, unfeathered heads and necks of male Wild Turkeys (*Meleagris gallopavo*) are generally thought to function in sexual selection. However, studies in other bird species have suggested that uninsulated body regions may serve an important role in heat dissipation. I test the heat-dissipation hypothesis in Wild Turkeys by experimentally reinsulating the heads and necks of Wild Turkeys as though they were feathered. The oxygen consumption, thermal conductance, cooling capacity, surface temperatures, and core temperature of control and reinsulated Wild Turkeys were compared at 0°, 22° and 35°C. Head insulation resulted in significantly increased rates of oxygen consumption, higher body temperatures, and decreased cooling capacities at 35°C, but had no significant effect at the other temperatures tested. It appears that behavioral changes at low temperatures, such as tucking the head under the back feathers, effectively prevent the heat loss that would otherwise be caused by the absence of feathers. However, if the head were feathered, turkeys at high temperatures would be unable to dissipate sufficient heat to maintain thermeostasis. Thus, given this finding for Wild Turkeys, it can no longer be said that in all cases bare heads in birds have evolved by sexual selection alone. Loss of head and neck feathering in Wild Turkeys and other birds may have allowed these species to take advantage of regions in time and space that previously were unexploitable due to the dangers of hyperthermia. *Received 22 June 1994, accepted 27 January 1995.*

ENDOTHERMS USUALLY MAINTAIN body temperatures above environmental temperature at considerable energetic cost. To save energy they reduce heat loss to the environment by insulating themselves completely with fur or feathers. Birds that have areas of unfeathered skin on their heads and necks are an unexplained exception to the pattern of complete insulation seen in other endotherms. In carrion-feeding birds, unfeathered heads often are assumed to be a hygienic adaptation (Welty 1975: 100). However, in species where the unfeathered areas are also brightly colored, sexually selected functions are usually suspected (Zuk 1991).

Despite some studies suggesting that these areas of bare skin maintain sublethal brain temperatures by dissipating heat via cephalo-cervical retes (Crowe and Crowe 1979, Crowe and Withers 1979, LaRochelle et al. 1982), thermoregulatory hypotheses for the evolution and maintenance of unfeathered skin rarely are considered. The heat-dissipation hypothesis is supported by correlative studies showing that unfeathered head and neck skin is maximally exposed at high temperatures and that in some taxa the size of unfeathered areas is greater at low latitudes where heat dissipation may be of greater importance (Crowe 1979, Buchholz 1994). Highly vascularized fleshy ornamentation presents a functional puzzle when species are distributed over a large latitudinal range in which they are exposed to both temperature extremes. Although these species may benefit by using their fleshy structures to dissipate heat under hot conditions, the uninsulated nature of these structures subjects the birds to extreme heat loss under cold conditions and heat gain in the presence of solar radiation. In this study, I test the possible thermoregulatory function of unfeathered head ornamentation in a species that commonly faces extremes of cold and heat, the Wild Turkey (*Meleagris gallopavo*).

Wild Turkeys occur over a broad range of temperature extremes from their southern limit in southern Mexico to their northern limits along the border of the United States and Canada (Dickson 1992). Males are twice as large as females, and have brightly colored unfeathered heads and necks (Buchholz 1995). In addition,

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this bare skin is covered with polyp like elaborations of the integument called caruncles. A thin dewlap extends from the mandible down to the neck. Perhaps most distinctive is the bare, distensible frontal process or snood that projects from the forehead at the base of the upper bill.

Fleshy head ornamentation in Wild Turkeys and other galliforms often is thought to be maintained by sexual selection (i.e. the structures function in mate choice and male-male competition). Ample empirical evidence supports this contention (Brodsky 1988, Boyce 1990, Hillgarth 1990, Ligon et al. 1990, Zuk et al. 1990a, b, Spurrier et al. 1991, Zuk et al. 1992, Buchholz 1995). A role in sexual selection, however, does not rule out concurrent functions for these structures in thermoregulation. Although both species of present-day turkeys (Meleagridinae) have unfeathered heads and necks, the common ancestors of modern turkeys presumably had feathered heads, as do most galliforms. Understanding why the unfeathered areas of modern turkeys are maintained, despite the possible costs in terms of heat loss, may explain why ancestral turkeys lost their head feathering over evolutionary time. In this study I experimentally insulate the heads and necks of Wild Turkeys to assess the thermoregulatory trade-offs that maintain unfeathered heads in this species.

METHODS

Subjects and equipment.—Eight two-year-old, male Wild Turkeys obtained as chicks from a game farm (L&L Pheasantry, Hegins, Pennsylvania) were used in the metabolic trials. Rearing conditions are described in detail elsewhere (Buchholz 1994). There is no difference in the metabolic rates of Wild Turkeys from game-farm or free-living sources (Gray and Prince 1988). The average body mass of the study individuals was 7.1 kg (range 6.4–8.1 kg). During the study period (29 June-27 September 1993) the birds were provided with feed (Purina Gamebird Maintenance, 12% protein) and water *ad libitum*. Subjects were denied food for 26 to 29 h immediately prior to each metabolic trial to insure that they were postabsorptive. Postabsorptive conditions are necessary to measure the basal or minimum rate of metabolism (McNab 1988a). Water was still available during the pre-trial period.

Oxygen consumption and total water loss were measured in an open system (described by McNab 1988b). The temperature of the 329-L metabolic chamber was regulated by pumping water from a water bath through the chamber's hollow walls. Room air

was drawn through the metabolic chamber, pumped into glass columns filled with soda lime (to remove CO_2) and silica gel (to remove H_2O), after which flow rates ($\bar{x}$ = 20.6 L/min) were measured by a Brooks Sho-Rate flowmeter. Subsequently, the airstream was sampled with an Applied Electrochemistry S-3A oxygen analyzer. The temperature and humidity of the room air varied little (23.5 ± SE of 0.0°C and 61.2 ± 0.2%, respectively). Humidity in the chamber was not controlled. The bird's evaporative water loss was measured gravimetrically (i.e. by weighing the silica gel). Core body temperature was measured by inserting a copper-constantan thermocouple, tipped with a thin layer of silicone, into the bird's intestine to a depth of 20 cm from the cloacal opening. This measurement was taken immediately before the subject was placed in the metabolic chamber and immediately after it was removed from the chamber. Six surface-temperature measurements were taken: feather, leg, body skin, head skin, frontal caruncle, and dewlap. Surface temperatures were measured with a bare-tipped thermocouple held against the appropriate spot, while the subject was still in its holding box before the trial and, again, while it was in the metabolic chamber at the end of a trial. Skin and feather surface temperatures were measured on the chest approximately 3 cm ventral to the carpal joint of the wing at rest. Leg temperature was measured immediately posterior to the third scale distal to the tarsal joint on the left or right leg, depending on which was accessible. Head skin temperature was measured on the back of the head at a point posterior to the lower mandible. Surface temperature of the frontal caruncles and dewlap were measured at the centers of these structures.

Different rates of physical activity across subjects and trials can make it difficult to detect the effect of experimental treatments on metabolic rate. Therefore, I minimized the bird's activity by conducting trials at night in the dark. Metabolic trials lasting 2.5 h were conducted between 1900 and 0200 EST. All subjects were given at least one day between trials. Individual turkeys were tested at the same time of day (either 1900 or 1100) across all treatments to minimize circadian effects on matched comparisons of metabolic rate. The first 30 min of each trial served as an equilibration period during which the bird calmed down after handling. The lowest rate of oxygen consumption (corrected to standard pressure and temperature) measured during each of the four subsequent 30-min periods was used to calculate an average metabolic rate for the entire trial. All individuals were given two 2.5-h habituation trials prior to the experimental trials. Usually, the subjects rested quietly during the experimental trials. The following three behavior patterns were recorded as present or absent through instantaneous sampling (Martin and Bateson 1986) every 30 min: standing; head tucked under feathers; panting. Observations were made with the aid of a flashlight through a small window in the chamber.

Experimental design.—To evaluate the potential thermoregulatory impact that head feathering would have on Wild Turkeys, I determined the thermal balance when the turkey's head was "bare" (see below), and when it was insulated as though feathered. To approximate the insulatory properties of head and neck feathering, the bare head and neck of the turkey were covered with a double layer (0.6 cm on head, 0.9 cm on neck) of acrylic sock (Adler "Casual Acrylic Crew"; 75% hi-bulk acrylic, 25% stretch nylon) with large holes for the eyes and the entire bill. The nostrils were never covered. Any irritational effects of the insulatory head covering on metabolic rate were controlled by placing a hood made of thin, nylon netting with little insulatory value on the heads of the "bare" individuals. The control head net and insulatory head socking were held in place with small alligator clips that attached to the back and chest feathers at the base of the neck. The efficacy of using head socking to approximate the insulation provided by normal feathering was determined by studying the warming curves of the feathered and unfeathered/reinsulated heads of domestic roosters (*Gallus gallus*; after Morrison and Tietz 1957).

Six dependent thermoregulatory variables may be affected by head insulation. Metabolic rate, as indicated by oxygen consumption ($cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$), is a measure of the work the animal does to maintain thermeostasis. The rate of evaporative water loss (g/h) is a measure of the heat lost via evaporation. Metabolic heat production (H_m) and evaporative heat loss (H_e) can be converted to common units (mW/g) to compare the cooling capacity of the animal in different treatments. Cooling capacity is the bird's ability to dissipate metabolically produced heat by evaporation. It is expressed as a percentage, calculated as the heat lost by evaporation divided by the heat produced by metabolism (100 H_e/H_m; Calder and King 1974). Total thermal conductance ($mW \cdot [cm^2]^{-1} \cdot [^\circ C]^{-1}$) measures all the heat lost by the animal, including evaporative heat loss, and is the inverse of insulation. It is estimated using the values for heat production, and ambient and body temperatures. Dry thermal conductance is a measure of all nonevaporative means of heat loss: radiation, convection and conduction. If total conductance is exceeded by heat production, heat is stored in the tissues of the animal and body temperature rises. Each of these components of thermal balance may be varied by the animal to cope with increased head and neck insulation.

Thermoregulatory trials were conducted twice for each turkey at each of three ambient temperatures (0°, 22°, 35°C), one time as a control, and the other with the turkey's head insulated. These temperatures were chosen to be below, within, and above, respectively, the zone of thermal neutrality (Gray and Prince 1988). The temperatures also are within the range that turkeys experience in the wild. I conducted 48 trials. This matched design compares the metabolic values of each turkey in the experimental treatment to the values obtained from the same bird in the control treatment, which serves to minimize the effects of interindividual variation on the effect of the experimental treatment. Due to scheduling conflicts in the laboratory, every turkey was tested at 0°C before it was exposed to the other temperatures. The presentation order of the trials at 22° and 35°C, and treatments at 0°, 22°, and 35°C was randomized. Repeated-measures ANOVAs (Abacus Concepts, Inc. 1989) were used to test the effects of body size ($\bar{x} = 6.7$ kg for small and 7.5 kg for large), chamber temperature, and head insulation on: oxygen consumption ($cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$); cooling capacity; total and dry thermal conductances ($mW \cdot [cm^2]^{-1} \cdot [^\circ C]^{-1}$); and changes in body and surface temperatures (°C). The effect of each 30-min sampling period was also included when oxygen consumption was the dependent variable. Treatment groups exhibited similar variances (F_{max} tests; all $P > 0.05$; Sokal and Rohlf 1981). Reported P-values were adjusted using Greenhouse-Geisser epsilon values (Abacus Concepts, Inc. 1989). This technique conservatively compensates for the use of repeated measures by adjusting the degrees of freedom. Thermoregulatory variables are reported as $\bar{x} \pm SE$, as appropriate.

RESULTS

The mass specific rate of oxygen consumption was significantly lower for large individuals across all temperatures ($\bar{x} = 0.4140 \pm 0.0070$ vs. 0.4730 ± 0.0130 $cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$; Table 1). The rate of metabolism was not significantly different for uninsulated and insulated turkeys at 0° and 22°C. However, at 35 °C, insulated turkeys exhibited a significantly higher average metabolic rate than uninsulated turkeys (Table 2, Fig. 1). A significant, three-way interaction of head insulation, temperature, and time period suggests that the effects of head insulation became more pronounced the longer the subject was exposed to the chamber conditions at hot temperatures.

Uninsulated turkeys demonstrate a significantly greater ability than insulated turkeys to dissipate excess metabolic heat by evaporation at 35 °C, but not at lower temperatures (Fig. 2). Total thermal conductance increased with temperature. It also was greater for insulated birds overall (Table 1, Fig. 3), but this difference was significant only at the highest temperature (Table 2). Dry thermal conductance decreased with increasing temperature in the uninsulated birds (Fig. 4). Insulated birds showed a similar pattern of conductances at 0° and 22°C, but had

TABLE 1. Partial results of repeated-measures AN-OVAs showing statistically significant sources of variation in the dependent measures (centered in bold) of thermal balance listed.

Source of variation	df	F-value
Oxygen consumption		
Size	1	5.96*
Insul × Temp	2	4.16*
Insul × Temp × Time	4	4.15*
Cooling capacity		
Temp	2	135.00***
Insul × Temp	2	8.87*
Thermal conductance (total)		
Insul	1	7.19*
Temp	2	367.00***
Insul × Temp	2	8.03*
Thermal conductance (dry)		
Temp	2	9.45*
Insul × Temp	2	7.96*
Core body temperature		
Insul	1	6.62*
Temp	2	22.10**
Insul × Temp	2	10.39*
Leg temperature		
Temp	2	150.00***
Feather temperature		
Temp	2	42.01***
Head-skin temperature		
Insul	1	12.09*
Temp	2	16.28***
Frontal-caruncle temperature		
Temp	2	6.39*
Dewlap temperature		
Temp	2	6.83*
Insul × Temp	2	7.79**

*, P < 0.05; **, P < 0.01; ***, P < 0.001.

significantly higher values than uninsulated birds at 35°C.

Head insulation resulted in significantly greater core-body temperature changes of birds at 35 °C, but not at the lower temperatures tested (Fig. 5). Head insulation served to keep head skin warmer at 0°C (uninsulated, 31.2 ± 1.0°C; insulated, 36.7 ± 0.3°C), but did not result in significantly higher skin temperatures at 22° and 35°C. Insulated turkeys at 22°C were significantly more likely to have increased dewlap temperatures than uninsulated birds (uninsulated, 32.1 ± 0.7°C; insulated, 35.2 ± 0.3°C insulated), but this was not true at 0° or 35°C. Body skin, feather, frontal caruncle, and leg temperatures all increased with increasing ambient

TABLE 2. Values ($\bar{x}$ ± SE) of dependent thermal variables in eight Wild Turkeys exposed to three ambient temperatures (°C) with their bare heads and necks uninsulated or insulated. Mean changes in temperature are presented (end-of-trial value minus beginning-of-trial value).

Dependent variable	0°C		22°C		35°C	
	Uninsulated	Insulated	Uninsulated	Insulated	Uninsulated	Insulated
Oxygen consumption (cm³ O₂·g⁻¹·h⁻¹)	0.45 ± 0.02	0.48 ± 0.24	0.41 ± 0.01	0.40 ± 0.01	0.43 ± 0.02**	0.50 ± 0.02**
Cooling capacity (%)	24.68 ± 3.31	29.51 ± 3.27	76.83 ± 5.47	84.90 ± 3.33	119.69 ± 7.33**	96.73 ± 4.32**
Thermal conductance (total) (mW·[cm²]⁻¹·[°C]⁻¹)	0.11 ± 0.01	0.12 ± 0.01	0.24 ± 0.01	0.23 ± 0.01	0.78 ± 0.03**	0.92 ± 0.06**
Thermal conductance (dry) (mW·[cm²]⁻¹·[°C]⁻¹)	0.09 ± 0.10	0.09 ± 0.12	0.06 ± 0.02	0.04 ± 0.01	−0.15 ± 0.05**	0.44 ± 0.05**
Core body temperature (°C)	−0.44 ± 0.17	−0.35 ± 0.15	−0.44 ± 0.12	−0.45 ± 0.11	0.36 ± 0.13**	1.49 ± 0.37**
Leg temperature (°C)	−16.96 ± 1.53	−19.15 ± 3.10	0.00 ± 0.62	−0.11 ± 0.69	2.54 ± 0.48	3.31 ± 0.64
Skin temperature (°C)	−2.39 ± 1.80	−2.71 ± 2.43	−1.21 ± 1.86	−0.16 ± 1.21	2.61 ± 1.34	2.48 ± 0.68
Feather temperature (°C)	−8.99 ± 1.67	−11.01 ± 1.49	1.15 ± 0.39	0.73 ± 0.63	5.45 ± 0.73	3.86 ± 1.54
Head-skin temperature (°C)	−3.03 ± 1.37*	0.71 ± 0.33*	−0.16 ± 0.45	1.11 ± 0.43	2.30 ± 0.73	2.96 ± 0.42
Frontal-caruncle temperature (°C)	−1.98 ± 1.05	−5.48 ± 4.56	−0.71 ± 0.70	1.59 ± 0.80	1.46 ± 0.63	3.94 ± 0.82
Dewlap temperature (°C)	−0.20 ± 0.77	−0.87 ± 0.56	−1.94 ± 1.06**	2.53 ± 0.52**	2.89 ± 0.78	2.70 ± 1.18

* Asterisks indicate statistically significant differences between uninsulated and insulated turkeys at given temperature. *, P ≤ 0.05; **, P < 0.01.
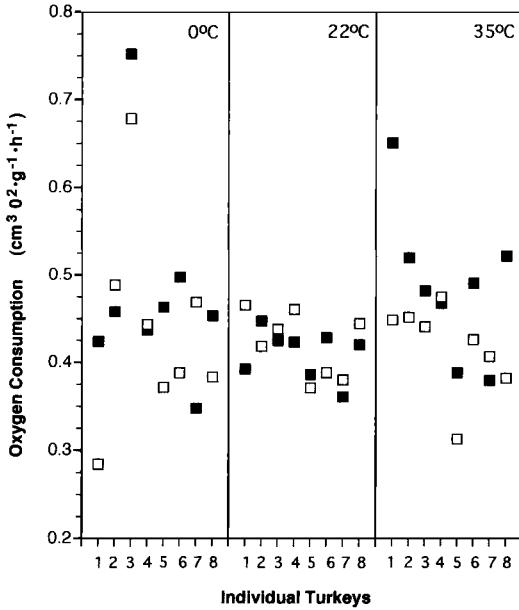
Fig. 1. Oxygen consumption of eight Wild Turkeys with heads uninsulated (empty squares) and then with heads insulated (filled squares) at three ambient temperatures. Turkeys presented in order of increased body mass.
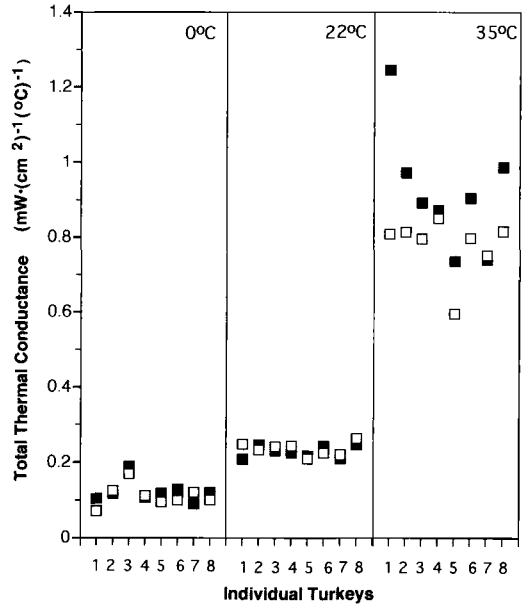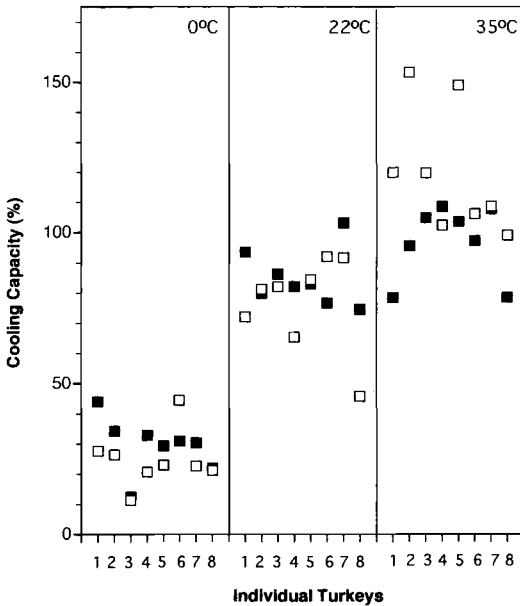
Fig. 3. Total thermal conductances of eight Wild Turkeys with heads uninsulated (empty squares) and then with heads insulated (filled squares) at three ambient temperatures. Turkeys presented in order of increased body mass.

Fig. 2. Cooling capacities of eight Wild Turkeys with heads uninsulated (empty squares) and then with heads insulated (filled squares) at three ambient temperatures. Turkeys presented in order of increased body mass.

temperatures, but were not affected by the insulation treatment (Table 1).

Across and within each temperature treatment, head insulation had no effect on the proportion of instantaneous observations during which the subjects were standing, panting, or had their head tucked in back feathers or under the wing (Mann-Whitney U-tests, $n = 16$, all $P > 0.05$). Panting only occurred at 35°C. The frequency of panting was difficult to observe because the birds often held their necks forward and down so that the view from the small window was blocked by the bird's body. Therefore, it was not possible to evaluate associations between panting frequency and thermal balance. Nevertheless, upon opening the chamber at the end of the 35°C trials, I observed panting and an elongated snood (only visible in uninsulated trials) in all individuals. Snood elongation did not occur at other temperatures.

Although the proportion of observations in which the subjects were standing was not influenced by the insulation treatment, the frequency of this behavior did have some effect on the dependent thermal variables. The frequency of standing had a significant positive correlation with head skin temperatures at 0°C
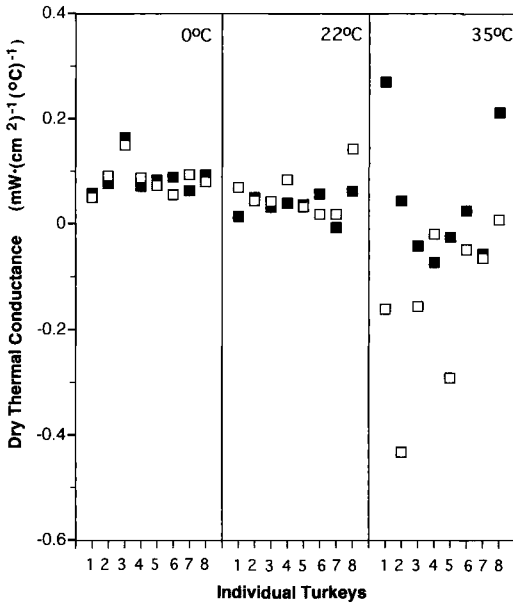
Fig. 4. Dry thermal conductances of eight Wild Turkeys with heads uninsulated (empty squares) and then with heads insulated (filled squares) at three ambient temperatures. Turkeys presented in order of increased body mass.
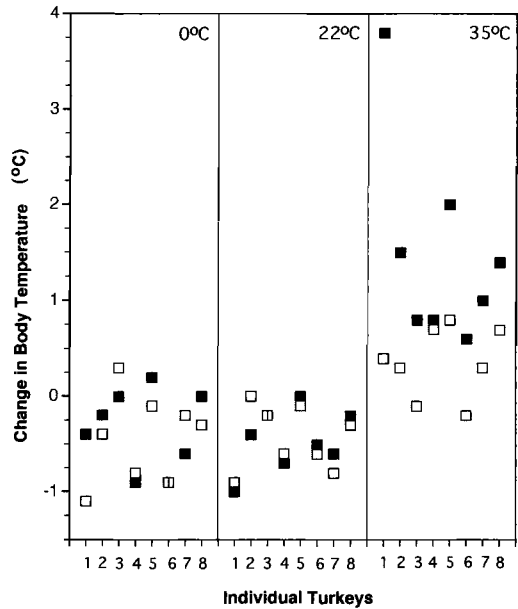

Fig. 5. Change in core body temperature of eight Wild Turkeys with heads uninsulated (empty squares) and then with heads insulated (filled squares) at three ambient temperatures. Individuals whose body temperature changed indentically when insulated and uninsulated are represented by a square containing a vertical line. Turkeys presented in order of increased body mass.

(both insulation treatments combined, $r_s = 0.54$, $P=0.05$) and may be associated with lower rates of metabolic heat production, although the latter correlation only approaches statistical significance ($r_s = -0.50$, $P=0.07$). At 22° and 35°C, feather temperature inversely correlated with standing frequency ($r_s = -0.66$, $P=0.01$ and $r_s = -0.52$, $P = 0.05$, respectively).

Head tucking occurred in 8 of 16 trials by six of the eight individuals at 0°C. Higher frequencies of head tucking were positively correlated with changes in dewlap temperature ($r_s = 0.50$, $P=0.05$), and negatively correlated with changes in skin temperature ($r_s = -0.58$, $P = 0.04$), changes in core body temperature ($r_s = -0.54$, $P = 0.05$), metabolic heat production ($r_s = -0.56$, $P = 0.05$), and both total and dry conductance ($r_s = -0.56$, $P= 0.05$ and $r_s = -0.66$, $P = 0.02$, respectively).

DISCUSSION

A dramatic cost of insulated heads and necks occurs in male Wild Turkeys at high temperatures. Insulated birds had higher metabolic rates and markedly increased core body temperatures relative to uninsulated males at the same

temperature. Although the insulated birds managed to increase dry and evaporative thermal conductances despite the head insulation, the lower cooling capacities of insulated birds is evidence of their inability to dissipate enough heat to offset metabolic heat production. These results demonstrate that the unfeathered heads and necks of male Wild Turkeys, and possibly the fleshy structures on the head, contribute to heat dissipation at high ambient temperatures.

Contrary to expectations, under cold conditions head and neck insulation did not significantly reduce thermal conductance or increase metabolic heat production. Under cold conditions, free-living Wild Turkeys often contract the skin at the back of their necks, effectively drawing the feathered skin at the base of the neck up and over much of the usually bare areas of the back of the neck (pers. obs.). The captive Wild Turkeys in my study exhibited similar behavior, possibly explaining the absence of a difference in thermal conductance between uninsulated and insulated birds at 0°C. Because winter starvation can be an important

source of mortality for turkey populations in the northern part of their distribution (Healy 1992a), reducing heat loss from the head may enhance turkey survivorship. At night, thermal conductance may be further decreased by tucking the head under the wing or back feathers. In my study, four of the eight uninsulated individuals at 0°C were seen with their heads tucked during at least one of the observation periods, and three of these had lower metabolic rates than the remaining individuals. La-Rochelle et al. (1982) found a similar effect of head tucking in Black Vultures (*Coragyps atratus*), which also have unfeathered heads. Additional studies of the effects of cold environmental conditions (e.g. low temperature, high wind speed, low insolation) and artificial head insulation on head tucking and thermal balance in Wild Turkeys are needed to confirm the efficacy of this tactic for reducing heat loss.

Anatomical adaptations used to modify heat loss have been described in other avian species. Ptarmigan (*Lagopus* spp.), which live at high latitudes and altitudes where the difference between body temperature and ambient temperature can be large (e.g. > 60°C), often have feathered legs and feet (Johnsgard 1983). Gulls (Laridae) have counter-current heat-exchange mechanisms that reduce heat loss from the feet under cold conditions (Baudinette et al. 1976). The Wood Stork (*Mycteria americana*) and Turkey Vulture (*Cathartes aura*) use their unfeathered legs to dissipate heat at hot temperatures and are able to enhance this mechanism of heat loss by defecating on their legs to promote evaporative heat loss (Kahl 1963, Hatch 1970). Ducks may use the large surface area of their bills to dissipate heat (Hagan and Heath 1980). The Wild Turkey is the only species in which the value of unfeathered heads and necks for heat dissipation has been demonstrated experimentally.

Previous studies of Wild Turkey metabolism have ignored the metabolism of Wild Turkeys at temperatures above 25°C (Gray and Prince 1988, Oberlag et al. 1990). The adaptive benefit of unfeathered heads demonstrated here suggests that peak effective temperatures during the reproductive season, especially in habitats without shade, may limit Wild Turkey distribution or population density. These results are reinforced by early studies on the temperature requirements of domestic turkeys. High ambi-

ent temperature (ca. 30°C) and exposure to direct sunlight may reduce male fertility by as much as 10% in broad-breasted bronze turkeys, the domestic breed most similar in appearance to Wild Turkeys (Kosin and Mitchell 1955). Wilson and Woodard (1955) found that all domestic turkeys were subject to hyperthermia at ambient temperatures above 32°C; this was particularly true of large males. In addition, body temperature and water consumption by domestic turkeys were inversely correlated with the percent of shade cover provided at ambient temperatures above 35°C (Wilson et al. 1955, Wilson and Woodard 1955). Wild Turkeys experienced heat stress at 35°C in the laboratory during my study. All males responded to hot chamber temperatures by panting, dropping their wings, and extending their necks and snoods. The smallest male even became frantic at the very end of both high-temperature trials and was removed immediately. Behavioral changes that occur in free-living wild males under hot conditions also suggest that activity is limited by high ambient temperatures.

Males call ("gobble") to attract females most often before dawn and during early morning (Hoffman 1990). This is especially true in the presence of clear skies (Healy 1992b), when males would risk greater heat and insolation later in the day. Mature male Wild Turkeys in northern Florida seem to avoid bright sun at any time of the year and, in summer, often are found standing in heavy shade with their dewlaps and necks bright red and extended, while panting heavily (pers. obs.). Also, the males are more reluctant to flee under these conditions and can be approached more closely than when it is cooler. Females engaged in gular fluttering under hot conditions but did not seem distressed by the heat. From these cursory observations it appears that the sexes differ in their susceptibilities to heat stress, possibly resulting in fitness conflicts between the sexes during the breeding season when males and females must be together.

Males gobble on warm days in winter, suggesting that they are more responsive to warm temperatures and less dependent on photoperiod to stimulate breeding than are females (Healy 1992b). Also, in most areas of their distribution, male turkeys exhibit a peak in gobbling behavior several weeks before females nest (reviewed by Hoffman 1990). The degree of sex

differences in reproductive timing may vary with latitude. Davis (1994: 117) found that Wild Turkeys in central Texas gobble synchronously with female receptivity, while southern Texas males peak in gobbling well before females are usually willing to mate. The remarkable ability of hen turkeys to store sperm for several months (Verma and Cherms 1964) may allow females to mate well before they would normally ovulate and thereby circumvent the reduction in fertility experienced by males at warmer temperatures (Kosin and Mitchell 1955). Of course sexual differences in reproductive timing might be explained by other ecological differences between the sexes. Nevertheless there are several lines of evidence to suggest that the daily and seasonal temporal patterning of male display behavior may be shaped to avoid overheating.

Males are faced with a thermoregulatory quandary under hot, sunny conditions. Resting quietly in the shade maintains sublethal body temperatures, but does not allow feeding, fighting for access to mates, or displaying to females. These latter activities are also functionally and adaptively necessary, but result in metabolic heat production and exposure to solar radiation. Field studies of the behavior of Wild Turkeys relative to environmental conditions, including radiative heat load and wind speed, are needed to understand how males trade-off thermal needs with feeding and mating success. The results of my study suggest that the bare heads and necks of male Wild Turkeys enable them to manage these conflicting goals more successfully.

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