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THERMOREGULATION IN TURKEY VULTURES: VASCULAR ANATOMY, ARTERIOVENOUS HEAT EXCHANGE, AND BEHAVIOR[1]

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Abstract. The vasculature of skin and of peripheral heat exchangers in Turkey Vultures (*Cathartes aura,* mass 1.4 kg) was studied in relation to peripheral temperatures and behavior at ambient temperatures (T_a) from 10°C through 50°C. The head's unfeathered skin contains thin-walled, anastomosing veins near the epidermis. Metatarsal skin has a similar venous plexus, but cutaneous vasculature from the wing's underside does not. Skin temperature (T_s) at the crown was close to T_a but T_s at the nape was close to body temperature (T_b). At both skin sites T_s changed with T_a. Investigation of deeper vasculature showed that the head has bilateral ophthalmic retia that probably cool the brain and eyes, as in other birds. In the wing, the basilica vein branches to form a venae comitantes, a mesh of anastomosing veins that separately surrounds the radial and ulnar arteries. A bypass vein is also present. The temperature profiles along the 10-cm length of this humeral plexus became steeper with decreasing T_a. At its distal end, temperature fell to 22°C at 10°C T_a, with the steepest observed gradient being 3.0°C/cm. In each leg, the tibial and fibular arteries closely contact two to four venae comitantes to form a simple rete, as in other species. This helps conserve body heat in cold but, as in the wing, is probably bypassed during heat stress. Behavior ranged from neck and wing retraction with a pale head and feet at low T_a, to neck and wing extension with a deep red head and feet at high T_a. Panting, gular flutter, and urohidrosis accompanied these responses at the highest T_as.

Key words: Cathartes aura; *Falconiformes; heat loss; heat transfer; peripheral vascular anatomy; skin vasculature; temperature regulation; Turkey Vulture.*

INTRODUCTION

Turkey Vultures (*Cathartes aura*) range from southern Canada throughout the United States to Central America. The populations at the northernmost edge of their range depart in autumn, but may still be exposed to winter storms when they return to their breeding areas (Hatch 1970), whereas populations in tropical and desert habitats experience humid and dry heat. Encountering a wide variety of climates, Turkey Vultures have apparently evolved diverse mechanisms to cope with thermal extremes.

Mechanisms that help Turkey Vultures tolerate cold include reducing body temperature to save energy and seeking shelter in caves (Heath 1962, Hatch 1970). High-temperature tolerance relies on both physiological and behavioral adaptations to dissipate heat. Turkey Vultures, when heat stressed in a metabolic chamber, regulated their body temperatures only by evaporation and reduced insulation, the chamber being too small to allow postural adjustments that increase heat loss (Arad and Bernstein 1988). In the field, however, Turkey Vultures exposed to high ambient

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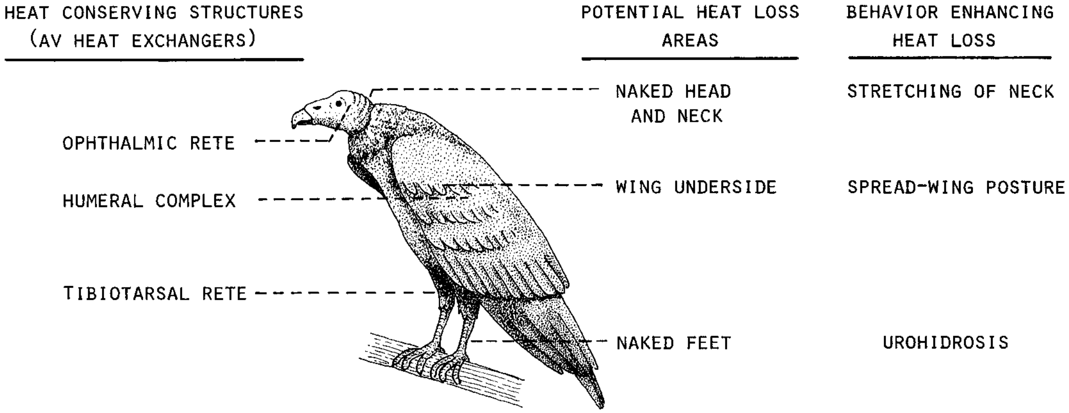

FIGURE 1. Summary of different areas and behaviors that are important in thermoregulation by Turkey Vultures.

temperature extend the unfeathered head and neck, expose the poorly feathered undersides of the wings, and urinate on the legs.

Arteriovenous, countercurrent heat exchangers are present in the heads, wings, and legs of many avian species (Midtgård 1988) and would be expected to help reduce heat loss during cold exposure. Reduced peripheral blood flow, especially in the naked skin of the head, neck, legs, and feet of Turkey Vultures, would also be expected to reduce heat loss, whereas increased cutaneous blood flow would accelerate heat dissipation during heat stress. In evaluating areas of unfeathered skin as potential heat-loss pathways, it is important to know their degree of vascularization. There are, however, no studies dealing with this topic, nor with the gross anatomy of arteriovenous (AV) heat exchangers, in Turkey Vultures.

The objectives of this study were therefore to describe the anatomy of the heat-exchange systems and skin vasculature in Turkey Vultures and thereby to establish a structural basis for part of their thermoregulatory repertoire (Fig. 1), then to correlate the morphology with preliminary temperature and behavioral observations thought to be part of that repertoire.

MATERIALS AND METHODS

ANATOMY

Five adult, captive Turkey Vultures (mean body mass 1.4 kg) were kept in an outdoor aviary and offered commercial bird-of-prey diet and water ad libitum, as previously described (Arad and Bernstein 1988). One bird that died during a previous study had been frozen. After thawing, its circulatory system was injected with latex (Microfil, Canton Biomedical Products), and then it was fixed by immersion in a mixture of alcohol, formaldehyde, and acetic acid (AFA). A second bird was anesthetized with inhaled halothane, cannulated in the brachial, cephalic, and sciatic arteries, and then given an overdose of anesthetic. The cannulae were perfused with warm, heparinized, isotonic saline, then with AFA. After fixation, samples of various skin areas and vascular complexes were removed and embedded in paraplast. The sections (10–12 μm thick) were stained with hematoxylin and eosin. The nomenclature applied to the observed vasculature follows the *Nomina Anatomica Avium* (Baumel et al. 1979).

TEMPERATURE MEASUREMENTS

To demonstrate the possible physiological significance of the morphological findings, we undertook preliminary measurements of temperature in presumed heat-exchange areas. To evaluate countercurrent heat exchange in the wing we measured temperature gradients along the humeral vascular complex in two vultures. On the day of an experiment, a bird was lightly restrained and locally anesthetized in the underside of one wing by subcutaneous injection of lidocaine (2%). A 15-cm-long incision was made in the humeral region and five insulated, 36-gauge, copper-constantan thermocouples were sutured to muscle with their junctions at fixed intervals along the humeral plexus. The skin was then sutured. To enable observations of skin temperatures in unfeathered regions of the head and neck, thermocouples were also inserted subcutaneously at the crown and the nape. For measurement of core body temperature (T_b), a thermocouple was placed in the cloaca to a depth of about 5 cm and tied to the rectrices.

The bird, with its eyes covered, was placed upright on a canvas sling mounted in a darkened, controlled-temperature chamber (±0.5°C). The legs protruded through holes in the sling and the wings were above the edges of the sling, so all four limbs remained unrestrained. The thermocouples extended through a small hole in the chamber wall and were connected to a digitizing data logger (Campbell Scientific, 21X) which calculated the means of 60 measurements from each thermocouple every minute. The data-logger output was directed to a microcomputer that displayed and recorded the temperatures to the nearest 0.01°C. Another thermocouple was placed near the bird in the chamber to measure ambient temperature (T_a), which was displayed on a digital thermometer (Bailey, Thermalert TH8). Prior to experiments, all thermocouples were calibrated against a mercury-in-glass thermometer having an accuracy (±0.1°C) traceable to the U.S. National Bureau of Standards.

The T_a was first set at 30°C (29.8–30.2°C), which is within the zone of thermal neutrality for this species. For one vulture, T_a was changed to 10°C (9.8–10.2°C) then to 40°C (39.8–40.2°C), whereas for the other vulture T_a was changed to 40°C then to 10°C. Each T_a was maintained until a thermal steady state was observed (1.0–1.5 hr); data were then recorded for at least 16 min.

BEHAVIORAL OBSERVATIONS

To gain preliminary information on behavior in relation to putative heat-exchange surfaces, an unrestrained Turkey Vulture was enclosed in the controlled-temperature cabinet with ample space to move about and change its posture. It was illuminated by the light from an incandescent lamp and observed from a darkened room through a small glass window in the chamber door. The bird was held at a T_a of 10, 20, 30, 40, 45, 50, or 53°C for 1.0–1.5 hr and posture, behavior, and color of the naked skin were observed and noted. Core T_b was measured in the cloaca at the end of the exposure to 53°C and after recovery at T_a of 35°C.

RESULTS

ARTERIOVENOUS HEAT EXCHANGERS

Head. The pattern of the major arteries and veins in the head (Fig. 2) conforms to that observed in other bird species. There are well-developed, bilateral ophthalmic retia with a high degree of AV contact (Fig. 3a). The numbers of arteries and veins in a rete are about 100 and 50, respectively. The main efferent arteries from the rete are the ophthalmotemporal and supraorbital arteries, which supply the eye and periorbital structures, but which also anastomose with the ethmoidal artery leading to the brain. The main venous tributaries to the rete are the ophthalmotemporal, supraorbital, and palpebral veins, which may receive blood from the eye, nasal cavity, and the skin surrounding the eye.

Wing. The wing is supplied and drained by the brachial artery and the basilica vein, respectively. The brachial artery divides into the radial and ulnar arteries. These parallel each other nearly throughout the length of the wing, as shown in Figure 4, and are each enmeshed in the humeral region by a surprisingly well-developed system of venae comitantes. In cross section this system appears to consist of four to nine veins in close contact with, and completely enveloping, each artery (Fig. 3b). In the distal part of the wing, the ulnar and radial arteries are each paralleled by only two veins (Fig. 4). The large, separate basilica vein, which constitutes the major drainage of the wing, courses independently in the distal part of the wing, anastomoses with the venae comitantes system of the radial and ulnar arteries near the elbow, and then bypasses the heat-exchange system in the humeral region.

Leg. As shown in Figure 5, most of the arteries in the lower leg are accompanied by veins, but the degree of AV contact is most extensive in the distal part of the tibial region. Sections of the cranial tibial vascular complex at this level show a large artery (the cranial tibial artery) and three collateral arteries (branches of the fibular artery, Fig. 3c) which are all in contact with two to four venae comitantes. Together these arteries and veins form a rete mirabile, although it is extremely simple.

SKIN VASCULARIZATION

Head and neck. Compared with the feathered part of the neck (Fig. 3d), the naked skin of the head is extremely well vascularized (Fig. 3e). In

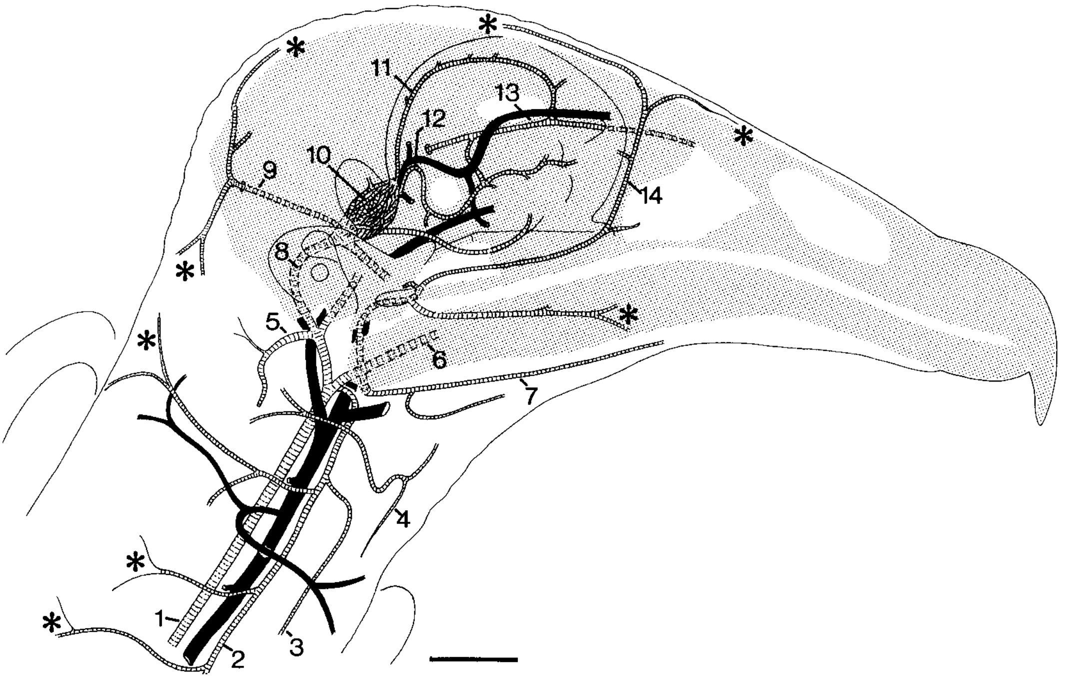

FIGURE 2. Outline of the major cephalic arteries in Turkey Vultures. For clarity, only some of the veins (black) have been shown. Arteries supplying the skin are marked with asterisks. 1, A. carotis interna; 2, A. comes N. vagi; 3, A. esophagealis descendens; 4, A. trachealis descendens; 5, A. occipitalis; 6, A. palatina; 7, A. lingualis; 8, A. ophthalmica externa; 9, R. occipitalis; 10, Rete ophthalmicum; 11, A. supraorbitalis; 12, A. & V. ophthalmotemporalis; 13, A. & V. ethmoidalis; 14, A. facialis. Scale bar equals 1 cm.

the superficial part of the cutaneous tissue, just below the epidermis, are one or two layers of thin-walled, anastomosing veins. Typical AV anastomoses (AVAs) as seen, for example, in the collar plexus of the pigeon (Baumel et al. 1983) and in the nasal mucosa of the duck (Midtgård 1984) were not observed to be associated with this cutaneous plexus. The venous plexus in the skin of the vulture's head appears instead to be supplied directly from slender arterioles originating from larger arteries located beneath a prominent subcutaneous layer of smooth muscle cells. The venous plexus in the skin of the crown and nape drains into the facial vein which appears to connect to the nasal vein, leading into the superficial occipital veins and into small branches leading directly to the jugulars.

Wing. Histological sections were made of the skin from several areas of the underside of the wing, but AVAs were not found, nor did the skin appear to have an unusual degree of vascularity that could be claimed to have special thermoregulatory importance.

Leg. The metatarsal skin is characterized by the presence of a dense network of veins located directly beneath the epidermis (Fig. 3f). The veins are a little smaller and appear more irregular in outline than those in the naked skin of the head. As in the head, the superficial venous plexus in the feet does not appear to be supplied by typical AVAs. AVAs were, however, encountered among the larger, more deeply located blood vessels.

TEMPERATURE MEASUREMENTS

Head and neck. As Table 1 shows, crown and nape skin temperatures were close to T_a and to T_b, respectively. Both were higher at 40°C T_a and lower at 10°C T_a than they were at 30°C T_a.

Wing. The temperature profiles recorded in one vulture are shown in Figure 6. Over the 10-cm length of the humeral plexus, temperature decreased, from T_b at the proximal end, to 38, 34, or 22°C at the distal end, at T_a of 40, 30, or 10°C, respectively. At 10°C T_a, the temperature decrease along the plexus was nonlinear, amounting to about 5°C in the first 6 cm, and

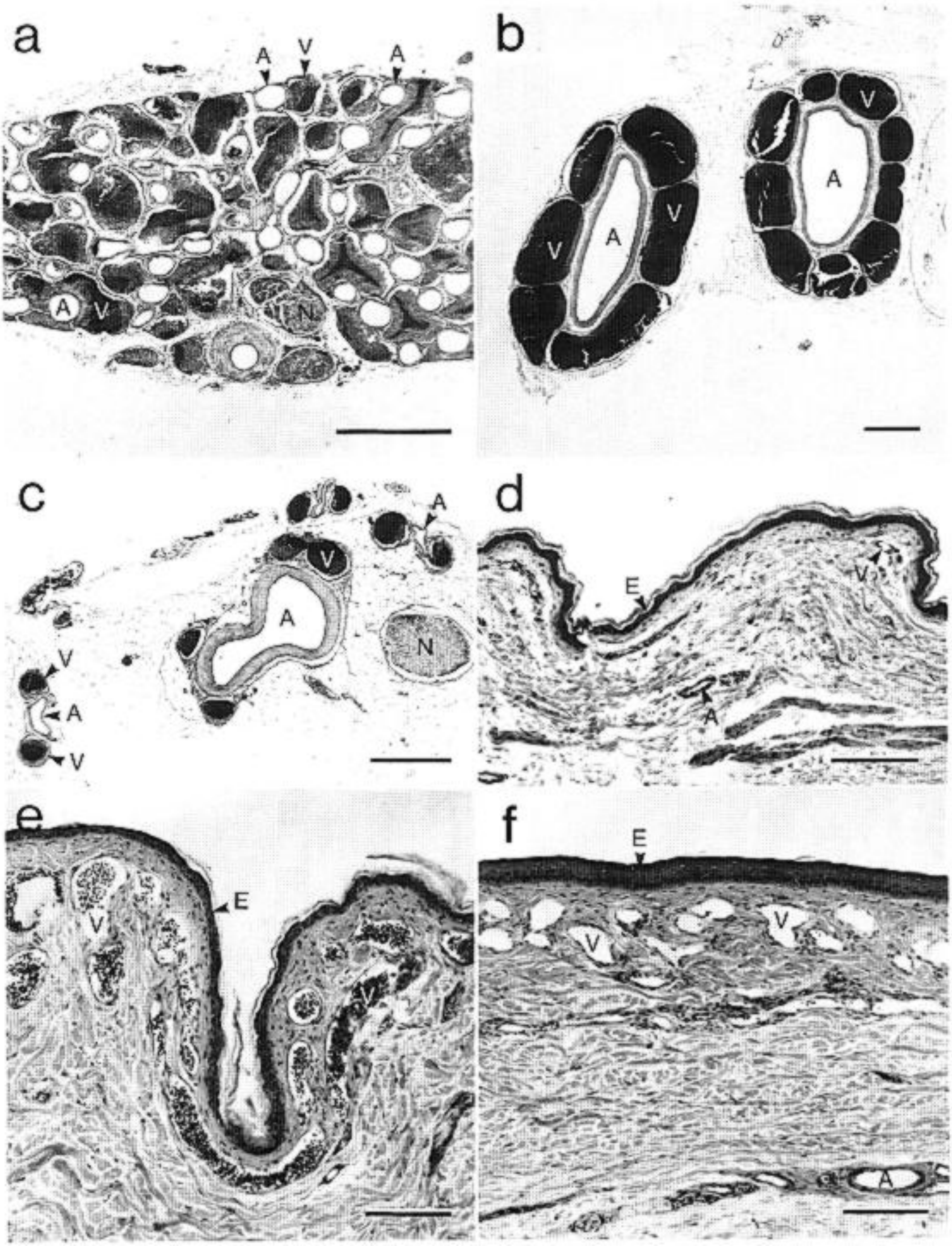

FIGURE 3. Histological sections of different skin areas and arteriovenous heat-exchange systems in Turkey Vultures. a, the ophthalmic rete. b, cross section of the arteriovenous heat-exchange system in the wing. c, section of the arteriovenous heat exchanger in the leg. d, skin on the feathered part of the neck. e, crown skin with a superficial venous plexus. f, section of the metatarsal skin. Abbreviations: A, artery; E, epidermis; N, nerve; V, vein. (Scale bars equal 0.5 mm in a–c and 0.1 mm in d–f.)

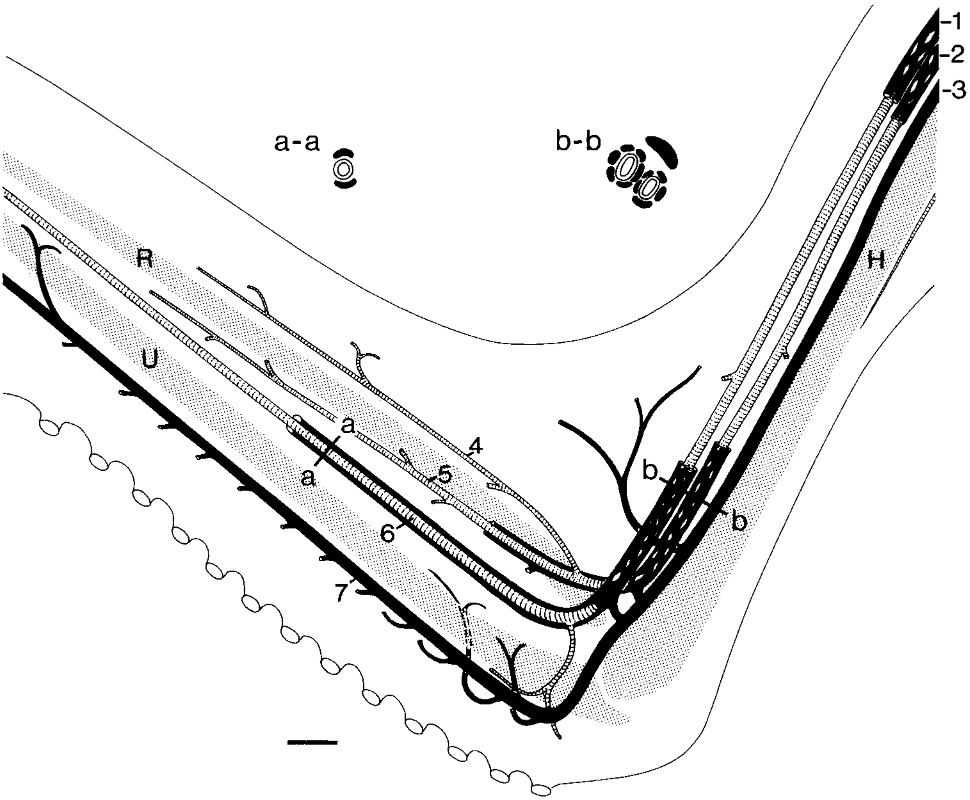

FIGURE 4. Diagram presenting ventral view of part of the right wing of a Turkey Vulture, showing the structure and location of the hypothesized arteriovenous heat-exchange system. Veins (black) have been drawn only in part. Drawings from sections have been added to illustrate arteriovenous proximity in the proximal (b-b) and distal parts (a-a) of the wing. 1, A. & V. ulnaris; 2, A. & V. radialis; 3, V. basilica; 4, A. radialis superficialis; 5, A. radialis profunda; 6, A. & V. ulnaris superficialis; 7, V. ulnaris profunda. H, humerus; R, radius; U, ulna. Scale bar equals 1 cm.

12°C in the last 4 cm. These changes correspond to thermal gradients of about 0.8°C/cm and 3.0°C/cm, respectively. The gradients at 30°C and 40°C were linear and amounted respectively to 0.46°C/cm and 0.25°C/cm. In the second vulture, the gradients were smaller, but changed with T_a in the same manner.

BEHAVIORAL OBSERVATIONS

At T_a of 10°C an unrestrained Turkey Vulture kept the undersides of its wings in close contact with its body, its head tilted downward, its neck retracted, and the skin of its crown wrinkled; the skin of its head and feet had a pale red color. At 20°C T_a, no visible changes occurred. At 30°C T_a, the head was horizontal, the crown was less wrinkled, the neck feathers were erect, and the head and feet skin were redder. At 40°C T_a, the wings were extended with their undersides not in contact with the body, the head was extended with the neck exposed, and their color was deep red. At 45°C T_a, the vulture adopted a drooped-wing posture, panted (160 min^{-1}) with its mouth open, and urinated on its legs. At 50°C T_a, synchronous panting and shallow gular fluttering were observed. At this stage, water was offered and the bird drank freely. At 53°C T_a, the wings were held farther from the body. After 90 min at this T_a, T_b was 41.7°C. When T_a was returned to 35°C, T_b decreased to 39.5°C but posture changed little.

DISCUSSION

This study provides a detailed description of the major blood vessels, AV heat-exchange systems,

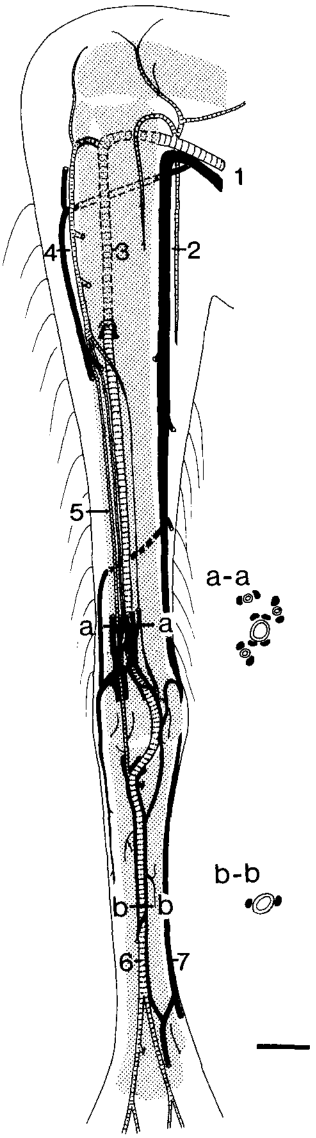

FIGURE 5. Cranial view of the main veins (black) and arteries in the right leg of a Turkey Vulture. The sections a-a and b-b illustrate arteriovenous proximity. 1, A. & V. poplitea; 2, A. & V. tibialis caudalis; 3, A. tibialis cranialis; 4, A. & V. fibularis superficialis; 5, Rete tibiotarsale; 6, A. & V. metatarsea dorsalis; 7, V. metatarsea superficialis medialis. Scale bar equals 1 cm.

and skin vascularization in the head, neck, wing, and leg of Turkey Vultures. The following discussion considers the findings as they relate to local and general thermoregulation.

TABLE 1. Core body temperature (T_b), and subcutaneous temperatures at the crown (T_{crown}) and nape (T_{nape}) at different ambient temperatures (T_a) in a Turkey Vulture. Values are the means of steady-state temperatures (range ± 0.2°C) recorded for at least 16 min. All temperatures in °C.

T_a	T_b	T_{crown}	T_{nape}
10	39.5	13.8	36.8
30	38.7	31.6	37.5
40	40.3	39.8	39.5

HEAD AND NECK

The head is equipped with well-developed ophthalmic retia, though the number of blood vessels in each rete is lower than that reported for other falconiform birds (Midtgård 1983). The ophthalmic retia of birds have been shown to cool the arterial blood to the brain (Kilgore et al. 1979, Bernstein et al. 1979), thus reducing the risk of heat stroke when T_b is elevated during heat exposure or exercise. It has also been suggested that the ophthalmic retia, like the AV heat-exchange systems in the limbs, reduce heat loss from the skin of the head in cold environments (Frost et al. 1975). Although this would seem to have particular value in a bird with an unfeathered head, it could function only for the periorbital skin, since the rete supplies blood only to this region (Fig. 2).

The vascularization of the bare cephalic skin in Turkey Vultures does not resemble that in the red skin of gallinaceous birds. Whereas the comb and wattles of domestic fowl contain a multilayered capillary network (Lucas and Stettenheim

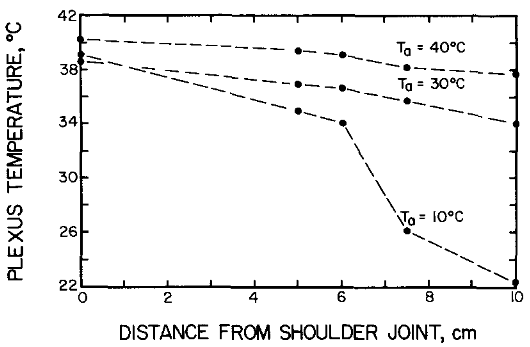

FIGURE 6. Temperatures recorded at intervals along the humeral vascular plexus, measured as the distance from the shoulder joint, in a Turkey Vulture exposed to ambient temperatures (T_a) of 40, 30, or 10°C.

1972), the naked skin of the vulture is characterized by large, superficial veins. The cephalic venous plexus of the Turkey Vulture is also different from the collar plexus of pigeons which is located subcutaneously and receives blood from AVAs (Baumel et al. 1983). The plexuses of both the pigeon and the vulture apparently function in thermoregulation.

It would be expected that vasodilation of the venous plexus in the skin of the head would aid heat loss during high-temperature stress, and that vasoconstriction would serve in heat conservation in the cold. These expectations are consistent with the behavioral observations: at high T_a, the head and neck were extended and the bare skin changed color to deep red; during cold exposure, the crown and nape skin appeared wrinkled and pale. In addition the subcutaneous temperature of the crown and nape increased significantly and approached core T_b during heat stress, whereas during cold exposure crown and nape skin temperatures decreased significantly, the decrease in the former being more pronounced than in the latter (Table 1).

Brain temperature in Helmeted Guineafowl (*Numida meleagris*) varied widely and was strongly affected by the thermal environment (Crowe and Withers 1979, Withers and Crowe 1980). These birds could regulate heat loss and heat gain through the naked head skin by extending and retracting their heads, and in this respect were similar to the Turkey Vultures in the present study and to Black Vultures studied previously by Larochelle et al. (1982). The cephalic skin thus seems to play an important role in temperature regulation by birds with unfeathered heads.

WING

The vascular anatomy of the wing has been studied in only a few species, and information about AV associations is limited to some penguins. In the proximal part of penguin forelimbs a rete mirabile with presumed heat-conserving function has been documented. Its arteries number from three to five in smaller species and about 15 in Emperor Penguins, *Aptenodytes forsteri* (Watson 1883, Trawa 1970, Frost et al. 1975). This structure has been implicated in heat conservation by penguins diving in cold water.

The present study demonstrates for the first time a similar heat exchanger in the wings of a strictly terrestrial, flying bird. In contrast with penguins, the heat exchanger in vulture wings is a well-developed venae comitantes system, completely enveloping the ulnar and radial arteries and equipped with a large shunt vein, the vena basilica. This venae comitantes system closely resembles that in the feet of ravens (Midtgård 1981) and in the fins of whales (Scholander and Schevill 1955).

Our temperature measurements along the humeral vascular complex (Fig. 6) strongly suggest that this structure functions as a heat exchanger. The temperature gradient increased from about 0.5°C/cm at thermoneutrality to about 3°C/cm in the distal segment during cold exposure. On heat exposure, the gradient decreased such that the temperature at the distal end was within about 2°C of T_b. We hypothesize that venous blood flow is directed through the plexus during cold exposure but bypasses it during heat exposure. The vulture results resemble those obtained in the forelimb of sloths by Scholander and Krog (1957), but the maximum gradient in the vulture was greater than in the sloth. The heat-exchange efficiency of the vulture's venae comitantes system is thus at least equal to that of the sloth's rete, but this needs confirmation by additional measurement of temperature and blood flow.

It has been suggested that the ventral side of the wing constitutes an important avenue for heat dissipation (Eliassen 1963); this is consistent with the spread-wing posture observed in heat-stressed Turkey Vultures. Our histological examination of underwing skin, however, did not show anything similar to the conspicuous vascularization of the head and leg. It is possible, especially during flight, that convection cools the large, superficially located veins, enhancing body cooling, and this would be enhanced by soaring in cooler air at high altitudes (Madsen 1930). It is also possible that evaporative or convective cooling of the dorsolateral thoracic surfaces is enhanced when they are exposed by wing spreading.

LEG

The AV heat-exchange system in the legs of Turkey Vultures is similar to that observed in cranes, ibises, and owls, and has been called a simple rete because of its small number of blood vessels (Midtgård 1981). As in other birds, the large tibial vein bypasses the heat exchanger and may be the preferred route for venous return when heat dissipation is called for.

The feet of birds are excellent dissipators of excess body heat (Steen and Steen 1965, Bernstein 1974, Kilgore and Schmidt-Nielsen 1975, Baudinette et al. 1976, Midtgård 1980) and are characterized by extensive skin vascularization and many AVAs (Midtgård 1986). In the present study, AVAs were found deep in the metatarsal skin, so they are apparently not involved in the filling of the superficial venous plexus. Nevertheless, this plexus undoubtedly has a thermoregulatory function, as suggested by the color changes of the metatarsal skin when T_a was elevated and by the habit of urinating on the legs during heat stress.

Kahl (1963) documented the latter phenomenon in heat-exposed Wood Storks (*Mycteria americana*) and showed that it plays a major role in temperature regulation in this species. Hatch (1970) verified Kahl's (1963) suggestion that urohidrosis also occurs in related New World vultures and found that, as in the Wood Stork, leg wetting contributes importantly to temperature regulation in heat-exposed Turkey Vultures. Taken together, leg vascular anatomy and urohidrosis in unrestrained Turkey Vultures point to an important role for the legs in this species' temperature regulation.

CONCLUSIONS

We have demonstrated extensive skin vascularization in the unfeathered head, neck, and feet; and well-developed AV heat exchangers in the head, wings, and legs of Turkey Vultures. We have provided preliminary support for the presumed thermoregulatory role of some of these structures by temperature measurements and behavioral observations. The unrestrained, freely moving bird regulated T_b over a wide range of T_a (10–53°C) by both physiological and postural adjustments. In contrast, Turkey Vultures confined in a metabolic chamber relied exclusively on physiological adjustments to maintain T_b (Arad and Bernstein 1988). Results of experiments under such conditions therefore represent only a part of the thermoregulatory adaptations of this species. The full range of adaptations explains the ability of Turkey Vultures to live in climates characterized by a wide range of thermal conditions.

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