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Urohidrosis and tarsal color in *Cathartes* vultures (Aves: Cathartidae)

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Abstract.—Heat-stressed New World vultures (Cathartidae) practice urohidrosis by excreting urate-rich urine on their tarsi and feet to decrease body temperature through evaporative cooling. Soft part colors are useful taxonomic characters in *Cathartes,* but dried urates obscure the color and pigmentation patterns of the tarsi and feet. I describe these characters in fresh specimens of *Cathartes aura* (Turkey Vulture), *C. burrovianus* (Lesser Yellow-headed Vulture), and *C. melambrotus* (Greater Yellow-headed Vulture) collected in Guyana. Species-specific differences in the melanic pigmentation of the tarsi and feet are revealed when urates are removed. The rosy-red intertarsal joints, which are normally unobscured by urates, may function in intraspecific signaling in all three species. The seasonality and geographic extent of urohidrosis in *Cathartes* are unknown.

Keywords: *Cathartes,* Guyana, tarsal color, intraspecific signaling, urohidrosis, vulture

Urohidrosis (Kahl 1963) is an unusual thermoregulatory behavior exhibited by all living species of New World vultures (Aves: Cathartidae) and storks (Aves: Ciconiidae). Heat-stressed vultures direct streams of urate-rich urine on their tarsi (Hatch 1970, Todd 1974), which decreases deep body temperature through evaporative cooling via arteriovenous heat exchangers (Arad et al. 1989). Dried urates exhibit low solubility in water and repeated episodes of urohidrosis result in a persistent chalky coating of the tarsi and feet. Urohidrosis plays an improbable role in the systematics of *Cathartes*, a well-defined clade of three vulture species restricted to the Western Hemisphere (Wetmore 1950, 1964, Johnson et al. 2016). Skin color variation and epidermal ornamentation of the head and neck correlate with known species boundaries and may have some utility in defining subspecies (Graves 2016). Tarsal and foot color may be similarly useful in characterizing populations but these traits are a mystery because naturalists have been reluctant to remove the chalky urates from freshly collected specimens.

Cathartes aura (Turkey Vulture), usually subdivided into six subspecies (Wetmore 1964, Kirk & Mossman 1998), breeds from southern Canada south through Middle America and the Greater Antilles to Tierra del Fuego and the Falkland Islands. Early naturalists described the tarsi and feet of eastern North American populations (*C. a. septentrionalis* and *C. a. meridionalis*) as flesh-colored (Catesby 1731, Wilson 1814, Swainson & Richardson 1831, Audubon 1834, Coues 1872) or dirty-white (Baird et al. 1905). The authors, however, failed to specify if the descriptions referred to dried or fresh specimens and washed or un-

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washed legs (Appendix 1). Subsequent descriptions of tarsal color of North American populations appear to paraphrase earlier accounts. Jamaican populations of the nominate subspecies (*C. a. aura*) were described as having ash-colored (Sloane 1725) or dull reddish tarsi covered with a white scurf (Gosse 1847). The Cuban population (*C. a. aura*) was described as having pinkish tarsi (Gundlach 1876). Tarsal color in the three South American subspecies (*C. a. jota, C. a. ruficollis,* and *C. a. falklandicus*) remains undescribed (but see Abbott 1861).

Wetmore (1964) determined that the "yellow-headed" vultures were composed of two broadly sympatric species based on size and plumage characters. *Cathartes burrovianus* (Lesser Yellow-headed Vulture) occurs in grassland, savannah, marsh, and mangrove swamp from eastern Mexico south to Argentina, Brazil, and Uruguay (Wetmore 1950, 1964). Tarsal and foot color (Appendix 2) have been reported from single specimens from Panama (*C. b. burrovianus*) and Argentina (*C. b. urubitinga*). Wetmore (1926), however, did not specify whether the urates had been removed before description. The third species, *Cathartes melambrotos* (Greater Yellow-headed Vulture), is widespread in primary forest in the Amazon River watershed and the Guianas (Wetmore 1964, Houston 1994). Relatively little is known about the natural history and morphology of this monotypic species (Graves 1992, Gomez et al. 1994, Graves 2016). Here I present the first descriptions of the tarsi and feet of *C. melambrotos* and *C. aura ruficollis* with comparative data for sympatric *C. burrovianus urubitinga* in Guyana.

Methods

Specimens of *Cathartes aura ruficollis* (2 ♂♂) and *C. burrovianus urubitinga* (2 ♀♀; 3 ♂♂) were collected from 16 to 21 October 2015 at Dadanawa Ranch, Upper Takutu-Upper Essequibo, Guyana (2°49.28′N; 59°31.34′W; 127 m above sea level). *Cathartes melambrotus* (3 ♀♀; 7 ♂♂) and an additional specimen of *C. aura* (1 ♀) were collected from 23 to 29 October 2015 in the Kanuku Mountains, ~45 km NNE of Dadanawa (3°12.20′N; 59°24.20′W; 109 m above sea level).

The tarsi and dorsal surfaces of the toes of specimens were swabbed for microbial analysis within 30 minutes of death. After swabbing, the legs were tagged and detached from the body at the intertarsal joint. I selected a single leg from each species for cleaning and photography. After soaking the leg in water for several minutes, I gently scrubbed away the urate coating with a soft toothbrush, patted the leg dry, and photographed it in natural light (45–60 m postmortem) with blue nitrile gloves as the background color standard. Color descriptions were based on photographs (Fig. 1). Legs were fixed in formalin and transported to the National Museum of Natural History (Washington, D.C.). The pattern of melanin deposition was examined in the entire series of specimens after storage in 70% ethanol for 2.5 years: *C. aura* (USNM 651995, 652005, 652028), *C. burrovianus* (USNM 651996, 652000, 652004, 652018, 652019), and *C. melambrotos* (USNM 652021–652026, 652029, 652030, 652032, 652299).

Reproductive condition of specimens was determined during specimen necropsy. Immatures were identified by the presence of a bursa of Fabricius (Glick 1983) and gray pigment on the maxillary ramphotheca (Henckel 1981). The fresh specimens (Fig. 1) described below were males in definitive plumage, with adult head and neck color, and no sign of gray bill pigment or a bursa.

Results

Cathartes aura ruficollis—Tarsi and feet of fresh specimens were extensively coated

Fig. 1. Washed tarsi and feet of three sympatric species of *Cathartes* vultures collected in Guyana—(top) *C. aura ruficollis* (♂, USNM 652005); (middle) *C. burrovianus urubitinga* (♂, USNM 652019); (bottom) *C. melambrotus* (♂ USNM 652021). Specimens were photographed 45–60 m after death.

Fig. 2. Tarsi and feet of *Cathartes aura ruficollis* (left to right; USNM 651095 ♂, 652005 ♂, 652028 ♀), collected in Guyana after 2.5 years of immersion in 70% ethanol.

with chalky urates, except for the rosy-red intertarsal joints. By the time the urates were removed, tarsal color (USNM 652005) had faded to creamy white, faintly tinted with pink (Fig. 1). Rapid fading indicated that the red hue was caused by hemoglobin in subcutaneous capillaries rather than carotenoid pigments. The small reticulate scales on the ventral surface of the tarsus, metatarsal pad (pulvinus metatarsalis), and plantar surfaces of the toes (pulvinus digitalis) were creamy white but obdurately soiled. The scutellate scales on the dorsal side of the distal phalanges were margined with brownish-black. Pigmentation patterns persisted after long-term immersion in ethanol (Fig. 2). Anecdotal observations suggest that the coverage of urates on tarsi and feet may be related to foraging ecology. Individuals of *C. a. aura* in Jamaica that scavenge and wade shorelines exhibit reduced urate deposits on tarsi and feet (see Fig. 2 in Graves 2019).

Cathartes burrovianus urubitinga—The urate-coated tarsi and feet of fresh specimens (Fig. 3) were similar in appearance to those of *C. aura*. The underlying color pattern, however, was notably different (Fig. 1). The proximal third of the tarsus was creamy white, tinted with faint yellow and pink near the intertarsal joint (USNM 652019). Reticulate scales at mid shaft were bordered distally with grayish-black. Dark pigmentation increased distally and the lower tarsus and toes were uniform grayish-black. The metatarsal pad and plantar surfaces of the toes were grayish-black rather than creamy white as in *C. aura*. The pigmentation pattern observed

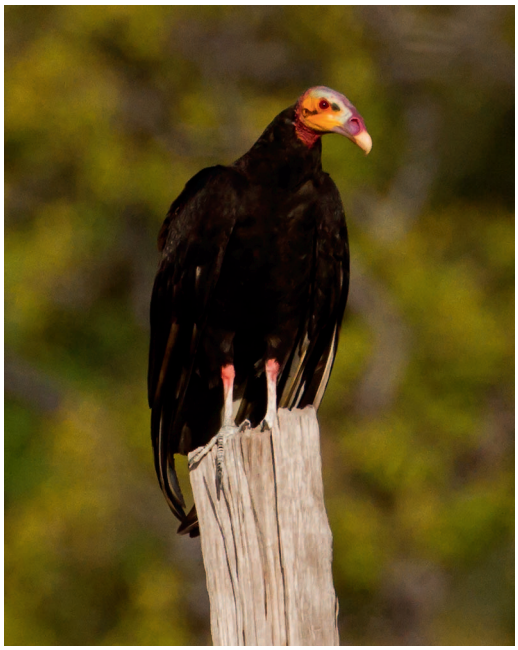

Fig. 3. *Cathartes burrovianus urubitinga*, Dadanawa Ranch, Upper Takutu-Upper Essequibo, Guyana. 6 January 2017. All three species of *Cathartes* in Guyana exhibited rosy-reds intertarsal joints that are visible under field conditions. Photograph courtesy of Cullen K. Hanks, Macaulay Library at the Cornell Lab of Ornithology.

on fresh specimens persisted after long-term immersion in ethanol (Fig. 4a).

Cathartes melambrotos—The tarsi and feet of the fresh specimen (USNM 652021) were coated with urates except for the rose-tinted intertarsal joints. After the urates were removed, the proximal four-fifths of the tarsus was creamy white with a faint pinkish tint near the intertarsal joint (Fig. 1). The small reticulate scales on the distal fifth of the tarsus were lightly pigmented with grayish-black. Scutellate scales on the dorsal surface of the toes were uniformly grayish-black; plantar surfaces of the foot were grayish-black. The distribution of melanic pigmentation of the tarsi and feet of *C. melambrotos* was roughly intermediate between that of *C. burrovianus* and *C. aura*.

Discussion

Avian soft parts pigmented with carotenoids, hemoglobin, and melanins frequently serve a signaling function (Negro et al. 2006, Bamford et al. 2010, Iverson & Karubian 2017). Hemoglobin flushing of highly vascularized skin has been reported in at least 20 avian families and 12 orders (Negro et al. 2006). In *Cathartes aura,* for example, naked head and neck skin ranges from dull pinkish-red to garnet red (Kirk & Mossman 1998, Graves 2016). Skin color changes rapidly from red to grayish-white when birds are stressed by handling. Color changes reverse when the birds are released (Henckel 1981). Fading and flushing of head color is caused by vasoconstriction and vasodilation, respectively, of subcutaneous capillaries (Arad et al.1989). During vasodilation, the skin assumes the bright red color of hemoglobin which masks the whitish collagen fibers in the subcutaneous connective tissue. Observations reported in this paper suggest that a similar process governs leg color of *Cathartes*. Brightly colored head and neck skin of *Cathartes* vultures have been hypothesized to play a role in intra- and interspecific signaling (Graves 2016). It is probable that hemoglobin-flushed intertarsal joints serve a similar purpose.

Finally, the seasonality and geographic extent of urohidrosis in *Cathartes* are unknown. If evaporative cooling is its sole function, then the frequency of urohidrosis should exhibit latitudinal, altitudinal, and seasonal gradients correlated with ambient temperature.

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Fig. 4. Tarsi and feet of (a) *Cathartes burrovianus urubitinga* (left to right; USNM 652000 ♀, 652004 ♂, 652018 ♂, 652019 ♂); and (b) *C. melambrotos* (left to right, USNM 652021 ♂, 650024 ♀, 652026 ♂, 652032 ♂) after 2.5 years of immersion in 70% ethanol. All specimens are adult except for USNM 652032, which possessed a cloacal bursa (10 × 6 mm).

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Appendix 1. Representative descriptions of tarsus and foot color of *Cathartes aura* (Turkey Vulture).

Source	Location	Subspecies by geography	Description
Gundlach (1876: 20)	Cuba	*aura*	"Los tarsos son violados, casi rosados; los dedos son pardos con escutelos morenos"
Sloane (1725: 294)	Jamaica	*aura*	"...the Toes...cover'd with Ash-colour'd Scales, and arm'd with brown blunt Claws..."
Gosse (1847: 9)	Jamaica	*aura*	"The feet are scaly, white; or rather dull reddish, covered more or less with a white scurf; the red hue is most apparent at the upper part of the tarsus; the claws are horny black."
Catesby (1731: 6)	Southeastern United States	*septentrionalis*	"...the legs short, of a flesh colour...their claws black..."
Wilson (1814: 102)	Eastern United States	*septentrionalis*	"...claws dark horn color; the legs are of a pale flesh color..."
Audubon (1834: 298)	Eastern United States	*septentrionalis*	"Feet flesh-coloured, tinged with yellow; claws black."
Swainson & Richardson (1832: 5)	Southern Canada	*meridionalis, septentrionalis*	"...the legs are flesh-coloured, and the claws have a dark horn-colour."
Coues (1872: 222)	United States	*aura, meridionalis, septentrionalis*	"...feet flesh-colored..."
Baird et al. (1905: 345)	United States	*aura, meridionalis, septentrionalis*	"...tarsi and toes dirty-white, tinged with yellow or flesh-color."

Appendix 2. Descriptions of tarsus and foot color of *Cathartes burrovianus* (Lesser Yellow-headed Vulture).

Source	Location	Subspecies	Description
Wetmore (1964:12)	Panama	*burrovianus*	"...front of tarsus dull greenish gray, rest dull white; toes fuscous black, claws fuscous."
Wetmore (1926:87)	Argentina	*urubitinga*	"...tarsus cartridge buff, shading to neutral gray on toes, where the interscutal spaces have a scurfy whitish appearance."