DOI: 10.7589/2016-07-162
Journal of Wildlife Diseases, 53(3), 2017, pp. 000–000

A Systematic Review of Carrion Eaters' Adaptations to Avoid Sickness

Daniel T. Blumstein,[1,3] **Tiana N. Rangchi,**[1] **Tiandra Briggs,**[1] **Fabrine Souza De Andrade,**[1] **and Barbara Natterson-Horowtiz**[1,2] [1]Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, California 90095-1606, USA; [2]The David Geffen School of Medicine, University of California, Los Angeles, California 90095, USA; [3]Corresponding author (email: marmots@ucla.edu)

ABSTRACT: Species that scavenge on dead animals are exposed to enhanced disease risks. Eight hypotheses have been suggested to explain how scavengers avoid becoming sick from their diet. We conducted a systematic review of the literature and found correlative support for four of the eight hypotheses but limited evidence of systematic studies of the hypotheses. We found no support that using urine to sterilize carcasses, having bald heads, eating rapidly, or food-washing behavior reduced disease risk in carrion eaters. With the exception of food washing, none of these hypotheses have been properly evaluated as an adaptation to avoid sickness from carrion. There is some support for having a specialized microbiome, having enhanced immunologic defenses, avoiding rotten food, and maintaining a low gastric pH to eliminate pathogens. Specialized immunologic defenses and having a low pH have the most support, but the diversity of mechanisms suggests that there is a great opportunity for even more detailed study. Increased knowledge in these mechanisms may provide biomimetic insights to help combat foodborne illnesses and enhance health.

Key words: Carrion eaters, disease avoidance adaptations, scavengers.

Introduction

Obligate and facultative scavengers are exposed to pathogens and toxic by-products of microbial metabolism. Eight hypotheses have been suggested to explain how scavengers avoid becoming sick from their diet. Understanding the diversity of these mechanisms is important because scavengers can disperse pathogens over long distances as they search for their next meal (Houston and Cooper 1975; Ohishi et al. 1979), scavengers play an important role in nutrient cycling in many ecosystems (DeVault et al. 2003, 2004), and from a biomimetic perspective (Benyus 1997), some of their defense mechanisms could potentially be used to improve human and veterinary medicine (Shaharabany et al. 1999). We systematically reviewed the literature on potential scavenger defense mechanisms and evaluated available evidence. We created search terms separately for eight previously hypothesized defense mechanisms: 1) taste before eat (Houston 1986); 2) specialized microbiome (Roggenbuck et al. 2014); 3) acid sterilization (Kushawha et al. 2009); 4) selective digestive tract (Wink 1995; Roggenbuck et al. 2014); 5) avoid rotten food (Houston 1986); 6) bald heads (Wink 1995); 7) specialized immune system (de la Lastra and de la Fuente 2007); and 8) rapid ingestion (Houston and Cooper 1975).

We systematically reviewed articles on carrion eaters' adaptations by using the Web of Science database (see PRISMA diagram in Supplementary Material). For each search topic, we narrowed the search by adding additional words until output was fewer than 300 articles; more inclusive searches yielded irrelevant articles. We first read the title and abstract of every article in the combined output. If the title or abstract mentioned a scavenger species, the words carrion, adaptation, feeding, behavior, or any other terms relevant to a hypothesized defense mechanism, we then read the full paper. For each included paper, we reviewed the bibliography of all articles and identified additional relevant papers. For all relevant papers, we also examined articles that cited these papers. A total of 30 papers provided some evidence for one or more hypothesized mechanism. Although popular articles and books suggest that carrion eaters have a variety of adaptations to avoid becoming sick, most evidence we found was correlative and focused on specific abilities in one or a few taxa. There were relatively few controlled experiments designed to properly test these hypotheses and determine whether these specific abilities are restricted to specific taxa. We discuss the evidence for each in the following.

Enhanced immunologic defenses

The best-supported defense mechanism involves specialized immunologic defenses toward pathogens encountered while scavenging. Animals are born with innate immunity (Cohen 1970), which includes physical barriers, such as skin, and immune surveillance adaptations, such as natural killer cells and phagocytic leukocytes. Later, animals acquire adaptive immunity (Abbas and Lichtman 2010), based on exposure to specific pathogens; this includes lymphocytes.

Seven case studies evaluated hypothesized immune mechanisms in mammals, birds, and reptiles (see Supplementary Table 1). These studies indicate that vultures have enhanced innate immunity that separates them from nonscavengers (de la Lastra and de la Fuente 2007). Research identifies differences between scavengers and nonscavengers in toll-like receptor (TLR) proteins (de la Lastra and de la Fuente 2007). The TLR proteins are a recognition receptor for pathogenic agents, and these proteins are a relatively well-studied innate immunologic mechanism. Vultures have specialized TLR1 proteins (de la Lastra and de la Fuente 2007), but TLR sequences and expression of facultative scavenging hyenas (Hyaenidae) were not significantly different than those found in other mammals (Flies et al. 2014). Vultures also possess a modified TANK binding kinase 1 protein (Chung et al. 2015) that enhances immune activity by stimulating interferon regulatory factors (IRF-3 and IRF-7) to prepare for a viral infection (tenOever et al. 2004). Alligators (*Alligator mississippienis*) kill and scavenge their food (Grigg and Kirshner 2015) and have leukocytes with antifungal properties against a variety of fungal pathogens. Their leukocytes also successfully inhibit the growth of 9 out of 11 tested pathogenic bacteria and have antiviral properties against human immunodeficiency virus and herpes simplex virus (Merchant et al. 2006).

Scavengers may also have enhanced adaptive immunity. Obligate scavengers, such as vultures, have more natural antibodies against botulinum toxin than do facultative scavengers (Ohishi et al. 1979). The development of botulinum antibodies is still an open question, and Ohishi et al. (1979) suggested that individuals exposed to botulism at an early age develop immunity. Merchant et al. (2013) studied the antibiotic-forming capabilities of captive Komodo dragons (*Varanus komodoensi*) and found their serum significantly inhibited the growth of gram-negative bacteria. However, not all facultative scavengers seem to be specialized. In a study comparing antibody responses in spotted hyenas (*Crocuta crocuta*) and domestic cats (*Felis catus*), there were no significant differences in magnitudes and patterns of humoral responses (Flies et al. 2012).

Low gastric pH

Vultures and some other scavengers have an especially low gastric pH that kills pathogens ingested from carrion (Houston and Cooper 1975), and there is evidence for selection of genes involved in the gastric acid secretion pathway in at least two species of vultures (Chung et al. 2015). Facultatively scavenging albatrosses (*Diomedea exulans*) also have low gastric pH, but this may also be an adaption for patchily distributed food, which requires rapid digestion for large meals (Grémillet et al. 2012).

Rapid ingestion

Houston and Cooper (1975) suggested that vultures eat quickly to prevent bacteria from forming spores. We found no evidence that this hypothesis has been scientifically evaluated. Indeed, feeding competition could select for rapid ingestion.

Acidic sterilization

Kushwaha et al. (2009) suggested that vultures release uric acid on their legs to kill pathogens they acquire while feeding and for cooling themselves. However, Hatch (1970) identified thermoregulatory benefits that turkey vultures obtained by wetting their legs with uric acid. We found no studies that formally tested whether urine or uric acid kills carrion-acquired pathogens.

Avoiding rotten food

Houston (1986) observed that turkey vultures avoided rotten food by recording the time it took for scavengers to find carcasses and the proportion of the carcass eaten. The proportion of the carcass eaten varied with carcass age. Turkey vultures primarily relied on their acute olfactory senses to locate food (Stager 1964); thus, some decomposition assists location, but when given a choice, vultures prefer 1-d-old carcasses over 5-d-old carcasses (Houston 1986). In contrast, brown tree snakes (*Boiga irregularis*) are more likely to eat a 2-d-old carcass over a 1-d-old carcass (Jojola-Elverum et al. 2001). Jojola-Elverum et al. (2001) hypothesized that brown tree snakes either actively seek rotten food or they are unable to find carrion that has not rotted. Brown tree snakes are hypothesized to have evolved salivary secretions that are specialized to neutralize toxic by-products of microbial metabolism within rotting food (Shivik 2006).

Bald heads

Although suggested in the popular literature (Stone 1993), we found no empirical evidence to support the hypothesis that bald heads are an adaptation to avoid becoming sick by facilitating cleanliness. Rather, two studies (Larochelle et al. 1982; Ward et al. 2008) provide evidence that baldness is a thermoregulatory adaptation.

Food washing

We found only two articles that studied whether washing food prior to consumption by scavengers reduces infection risk; neither supported this hypothesis. In nonscavenging macaques (*Macaca fuscata fuscata*), individuals that washed their food had reduced geohelminth infections (Sarabian and MacIntosh 2015). However, a critical analysis of food washing in raccoons (*Procyon lotor*), a facultative scavenger, found no evidence supporting an antidisease function. Lyall-Watson (1963) suggested washing simulates catching live prey, and this stimulates their appetite when eating carrion. More studies, such as those conducted with macaques (Sarabian and MacIntosh 2015), are warranted.

Microbiome

A specialized facial and gut microbiome may prevent population growth of pathogens. Vultures are exposed to fusobacteria and clostridia in their diet, and their hindgut microbiome is less diverse than their facial microbiome, suggesting that bacteria are either killed or outcompeted in the gut (Roggenbuck et al. 2014). Moreover, New World vultures have similar microbial communities, suggesting that certain microbial communities may be an adaptation to avoid diet-induced illness (Roggenbuck et al. 2004).

Summary

Despite its popular appeal, we found no consistent support that behavioral defenses are mechanisms that help scavengers avoid becoming sick when they eat carrion. However, we found some support that physiologic defenses have evolved to avoid sickness. We acknowledge that very few studies directly and formally evaluated these hypotheses in scavengers and that a recent study of food washing in a nonscavenger found that washing food reduced infection (Sarabian and MacIntosh 2015). We also acknowledge that some conclusions are pathogen specific. Nonetheless, this systematic review summarizes the current state of knowledge and identifies knowledge gaps, among them the need for properly designed studies to evaluate formally these hypotheses in multiple species.

More studies of microbial defenses are likely to be promising and may help create novel applications in both human and veterinary medicine. There is the potential to incorporate TLR expression to reduce susceptibility to specific pathogens. There is also bioprospecting potential in copying the distinct components of vulture TLR proteins. Although the function of the TLR1 structural differences has not been characterized, in FGriffon vultures, highest TLR1 expressions were in locations integral to immunologic defenses, including the kidney, small intestine, and peripheral blood mononuclear cells. Thus, we encourage further research of the function of TLR structural differences, which may ultimately lead to biomimetic applications, depending on what future findings suggest. Further study of the amino acid sequence polymorphisms of the TANK binding kinase 1 of the immune pathway could also have medicinal applications.

Acknowledgments

We thank the Blumstein lab and two very constructive reviewers for comments on previous versions. T.B. was a University of California–Historically Black Colleges and University Fellow; F.S.D.A. was supported by the Brazilian Ministry of Education's Coordination for the Improvement of Higher Education Personnel program; and D.T.B. is supported by the U.S. National Science Foundation.

SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at http://dx.doi.org/10.7589/2016-07-162.

LITERATURE CITED

Abbas AK, Lichtman AL. 2010. *Basic immunology: Functions and disorders of the immune system*, 3rd Ed. Elsevier Health Sciences, Philadelphia, Pennsylvania, 312 pp.

Benyus JM. 1997. *Biomimicry: Innovation inspired by nature*. William Morrow, New York, New York, 308 pp.

Chung O, Jin S, Cho YS, Lim J, Kim H, Jho S, Kim HM, Jun J, Lee H, Chon A, et al. 2015. The first whole genome and transcriptome of the cinereous vulture reveals adaptation in the gastric and immune defense systems and possible convergent evolution between the Old and New World vultures. *Genome Biol* 16: 215.

Cohen GM. 1970. *Studies on the resistance of roosters and vultures to type A botulinal toxin*. PhD Dissertation, Florida State University, Tallahassee, Florida, 168 pp.

de la Lastra JM, de la Fuente J. 2007. Molecular cloning and characterisation of the griffon vulture (*Gyps fulvus*) toll-like receptor 1. *Dev Comp Immunol* 31: 511–519.

DeVault TL, Brisbin, Jr IL, Rhodes, Jr OE. 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Can J Zool* 82:502–509.

DeVault TL, Rhodes OE Jr, Shivik JA. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.

Flies AS, Grant CK, Mansfield LS, Smith EJ, Weldele ML, Holekamp KE. 2012. Development of a hyena immunology toolbox. *Vet Immunol Immunopathol* 145:110–119.

Flies AS, Maksimoski MT, Mansfield LS, Weldele ML, Holekamp KE. 2014. Characterization of toll-like receptors 1–10 in spotted hyenas. *Vet Res Commun* 38:165–170.

Grigg GC, Kirshner D. 2015. *Biology and evolution of crocodylians*. CSIRO Publishing, Clayton, Victoria, Australia, 672 pp.

Grémillet D, Prudor A, Le Maho Y, Weimerskirch H. 2012. Vultures of the seas: Hyperacidic stomachs in wandering albatrosses as an adaptation to dispersed food resources, including fishery wastes. *PLoS One* 7: e37834.

Hatch DE. 1970. Energy conserving and heat dissipating mechanisms of the turkey vulture. *Auk* 87:111–124.

Houston DC. 1986. Scavenging efficiency of turkey vultures in tropical forest. *Condor* 88:318–323.

Houston DC, Cooper JE. 1975. The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *J Wildl Dis* 11: 306–313.

Jojola-Elverum SM, Shivik JA, Clark L. 2001. Importance of bacterial decomposition, and carrion substrate to foraging, brown treesnakes. *J Chem Ecol* 27:1315–1331.

Kushwaha S, Kanaujia A, Basu D. 2009. Nature's scavengers: Vultures. *Res Environ Life Sci* 2:185–192.

Larochelle J, Delson J, Schmidt-Nielsen K. 1982. Temperature regulation in the black vulture. *Can J Zool* 60:491–494.

Lyall-Watson MA. 1963. A critical re-examination of food "washing" behaviour in the raccoon (*Procyon lotor* Linn.). *J Zool* 141:371–393.

Merchant M, Henry D, Falconi R, Muscher B, Bryja J. 2013. Antibacterial activities of serum from the Komodo dragon (*Varanus komodoensis*). *Microbiol Res* 4:16–20.

Merchant ME, Leger N, Jerkins E, Mills K, Pallansch MB, Paulman RL, Ptak RG. 2006. Broad-spectrum antimicrobial activity of leukocyte extracts from the American alligator (*Alligator mississippiensis*). *Vet Immunol Immunopathol* 110:221–228.

Ohishi I, Sakaguchi G, Riemann H, Behymer D, Hurvell B. 1979. Antibodies to *Clostridium botulinum* toxins in free-living birds and mammals. *J Wildl Dis* 15:3–9.

Roggenbuck M, Schnell IB, Blom N, Baelum J, Bertelsen MF, Sicheritz-Pontén T, Sørensen SJ, Gilbert MT, Graves GR, Hansen LH. 2014. The microbiome of New World vultures. *Nature Commun* 5:5498.

Sarabian C, MacIntosh AJJ. 2015. Hygienic tendencies correlate with low geohelminth infection in free-ranging macaques. *Biol Lett* 11:20150757.

Shaharabany M, Gollop N, Ravin S, Golomb E, DeMarco L, Ferreira PC, Boson WL, Friedman E. 1999. Naturally occurring antibacterial activities of avian and crocodile tissues. *J Antimicrob Chemother* 44: 416–418.

Shivik JA. 2006. Are vultures birds, and do snakes have venom, because of macro- and microscavenger conflict? *BioScience* 56:819–23.

Stager K. 1964. The role of olfaction in food location by the turkey vulture (*Cathartes aura*). *Los Angeles County Mus Contrib Sci* 81:1–63.

Stone LM. 1993. *Vultures*. Carolrhoda Books, Minneapolis, Minnesota, 48 pp.

tenOever BR, Sharma S, Zou W, Sun Q, Grandvaux N, Julkunen I, Hemmi H, Yamamoto M, Akira S, Yeh WC, Lin R, Hiscott J. 2004. Activation of TBK1 and IKKε kinases by vesicular stomatitis virus infection and the role of viral ribonucleoprotein in the development of interferon antiviral immunity. *J Virol* 78:10636–10649.

Ward J, McCafferty DJ, Houston DC, Ruxton GD. 2008. Why do vultures have bald heads? The role of postural adjustment and bare skin areas in thermoregulation. *J Therm Biol* 33:168–173.

Wink M. 1995. Phylogeny of Old and New World vultures (Aves: Accipitridae and Cathartidae) inferred from nucleotide sequences of the mitochondrial cytochrome b gene. Z. *Naturforsch* 50:868–882.

Submitted for publication 12 July 2016.
Accepted 22 October 2016.