

Are Vultures Birds, and Do Snakes Have Venom, because of Macro- and Microscavenger Conflict?

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I outline models that describe vertebrate and microbial competition for carrion resources and help explain the resultant morphologies observed in extant vertebrate scavengers. Odors from microbial decomposition signal the presence of a carcass to vertebrate scavengers. Therefore, microbes must consume carcasses rapidly or evolve toxic defenses to protect themselves and their resource from their vertebrate competitors. Similarly, macroscavengers must evolve traits that allow rapid detection of carcasses or develop chemical defenses against microbial toxins. My modeling suggests that the most efficient macroscavenger adaptations increase the probability of carcass detection, which explains why highly vagile species, such as vultures, are the most obligate of vertebrate scavengers. Empirical data from vultures and from a scavenging snake species suggest that evolutionary pressures favor detection maximizers relative to toxification minimizers in competitive interactions for carcasses. However, detoxification mechanisms allow safe consumption of carrion and may have influenced the development of the complex digestive enzymes and delivery systems now seen in minimally vagile scavenging snakes.

Keywords: Boiga irregularis, carrion, Cathartes aura, decomposition, scavenging

Because humans have a distaste for rotting carcasses and a bias toward charismatic predation behaviors, the importance of carrion as an intermediate actor in energy transfer in ecosystems has been little appreciated and inadequately studied (Putman 1983, Shivik 1999, DeVault et al. 2003). In some ecosystems, predation is not the major mortality factor. Mammalian predators on ungulates in the Serengeti, for example, account for only 36 percent of carrion biomass (Houston 1979); in some systems such predators may account for only 60 percent of the production of mammals during any one year (Putman 1976), with most canopy-dwelling mammals probably dying from causes other than predation (Houston 1994). Thus, an ecologically significant amount (possibly 40 to 64 percent) of energy transfer in ecosystems may pass through a carrion intermediate (DeVault et al. 2003).

Competition for rotting carcasses is similar to that described for rotting fruits, seeds, and meat (Janzen 1977). That is, competition for carcass resources occurs not only among vertebrate macroscavengers (e.g., vultures, hyenas, wild dogs) but also among invertebrate microscavengers (bacteria, fungi) that colonize and attempt to sequester carcass resources. The objective of this article is to develop and evaluate simple, empirically based models that describe the evolutionary implications of competition between micro- and macroscavengers for the quantitatively important carrion

resource. These models provide a framework for understanding selective pressures that resulted in the development of chemical defenses in invertebrate scavengers and specialized morphologies in vertebrate scavengers.

A simple model of microscavenger resource use

Yeast (*Saccharomyces* spp.) growth in a glucose solution is a simple model for microscavenger growth on a finite resource (e.g., a carcass) and provides an intuitive theoretical underpinning for describing competitive pressures on multiple taxa as carcasses are consumed by microscavengers. A simple model of microbiotic scavenging can be described by the conversion of glucose into by-products during fermentation by yeast:



Growth occurs rapidly as organisms reproduce and consume resources exponentially until the environment is no longer suitable for reproduction (figure 1a; Papazian 1984). Given a finite resource, the curve describing glucose consumption

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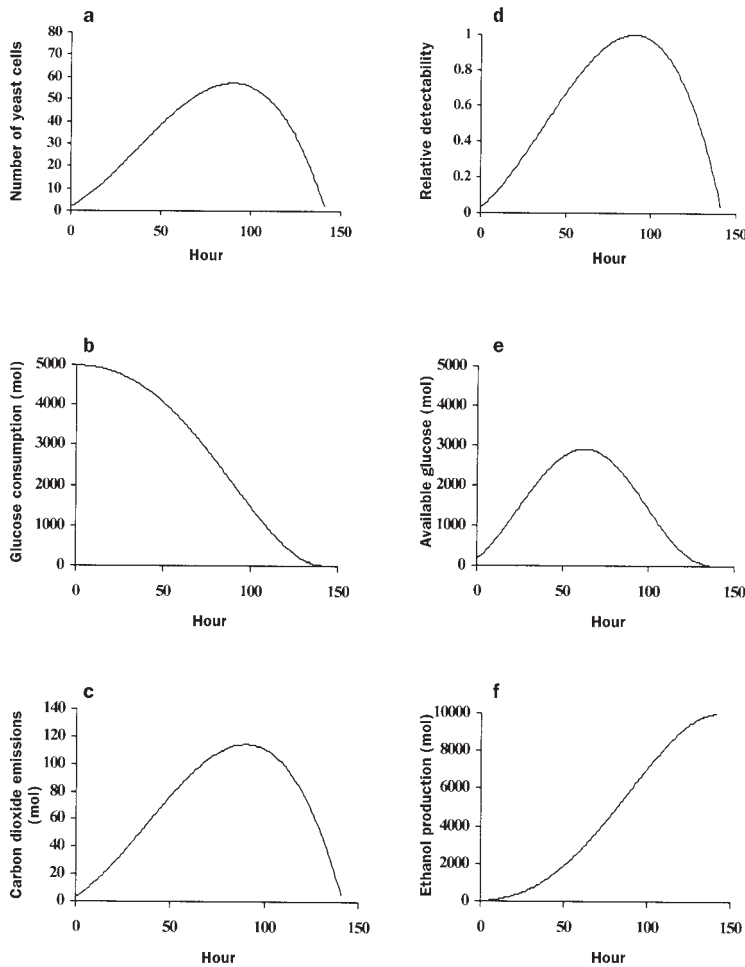


Figure 1. (a) Yeast growth in a glucose medium (data are modified from Papazian 1984). (b) Food resource consumption by yeast under initial conditions of 5000 moles (mol) of glucose, derived from (a). (c) Carbon dioxide emissions from yeast in a contained environment consuming 5000 mol of glucose, derived from (a). (d) Temporal change in probability of detection of a microbiotic scavenger consuming a resource constructed by scaling curve (c) to peak at 1.0. (e) The expected null model of resource consumption by a microbiotic scavenger based on detection due to carbon dioxide emission and availability through time of the resource formed by multiplicatively combining the curve in (b) with (d). (f) Cumulative production of the toxicant ethanol through time, based on production according to simple fermentation of 5000 mol of glucose.

is derived from the population growth curve for yeasts in the system (figure 1b). As glucose is consumed, carbon dioxide (CO_2) is emitted according to the fermentation equation and as derived from the glucose consumption curve (figure 1c). Interestingly, the CO_2 emission curve predicted in this model closely follows CO_2 emissions from rotting carcasses in the field (Putman 1978). The products of microbial decomposition attract vertebrates to edible carrion (DeVault et al. 2004). Assuming that the rate of CO_2 emission through time is directly related to the probability that macroscavengers with sensory sensitivity to the volatile by-product of fer-

mentation (CO_2 in this theoretical system) will detect metabolizing microbiotic scavengers on a carcass resource, the period of the most rapid consumption of the resource is also when the signal of a carcass to competing scavengers is the greatest. Thus, the probability that macroscavengers will detect microscavengers can be described by scaling figure 1c such that the point of highest gas emission is the point of highest detection probability (figure 1d).

Within the model system thus described, the expected model for macroscavenger detection and consumption of a carcass resource is a combination of the probability of a resource's being detected and the energy associated with the resource through time. That is, in this framework the null model of expected consumption is $C = R \times D$, where C is predicted macroscavenger consumption, R is resource availability, and D is the probability of detection of the resource by macroscavengers. Thus, consumption is predicted by combining the resource availability curve (figure 1b) with the detection probability curve (figure 1d) to produce the expected consumption curve (figure 1e). This model is useful in describing the changes in detection probability and reward through time; before microscavenger invasion, carcasses retain the highest levels of nutrient value but are not easily detected by macroscavengers. As rotting continues, detectable volatiles increase as the resource is rapidly consumed by microscavengers. Eventually, detection probability and value decrease until the carcass is minimally consumed by vertebrate scavengers.

Such models are useful for understanding the temporal use of carcass resources, but additional parameters are required for more realistic description of the competitive pressures on, and adaptations by, micro- and macroscavengers. Microscavengers may compete best with vertebrate species by colonizing and consuming resources rapidly enough to preclude carcass detection by macrocompetitors. However, because of the physiological constraints of metabolism, consumption by microscavengers results in by-products that signal decomposition,

and increased rates of microscavenger consumption result in an increased probability of detection by macroscavengers.

To outcompete macroscavengers, microbes must more rapidly colonize and consume a carcass or, alternatively, produce toxins that help protect the microscavengers and the food resource from competitors (Janzen 1977). Clearly, microbial adaptations have evolved toward chemical protection; the vagility of reproducing microbes is limited, but a wide array of potent toxins are familiar in such organisms as *Bacillus stearothermophilus*, *Clostridium perfringens*, *Clostridium botulinum*, *Escherichia coli*, *Staphylococcus aureus*, *Shigella*

dysenteriae, *Salmonella typhi*, and others, which all produce toxins that are harmful to mammals, birds, and reptiles. Therefore, an effective defense for microscavengers is to develop chemical defenses and by-products of metabolism that prevent other species from consuming the microbes and the resource they inhabit. In the fermentation model described above, the evolution of CO_2 is simultaneous with the production of ethyl alcohol, a toxicant. Through time, ethanol is produced according to the fermentation equation and as shown in figure 1f. Thus, a more accurate representation of expected consumption includes a toxic by-product: $C = (R - T) \times D$, where predicted consumption (C) equals the difference between the amount of nutritive resource available (R) and the penalty of neutralizing a toxicant (T), multiplied by the detection probability (D) of the resource. Assuming an energetically equivalent (1:1) penalty for detoxification relative to the reward of the resource, the addition of a toxicant into the model significantly decreases the predicted consumption (figure 2a).

Macroscavenger response to microscavenger defenses

The models developed thus far can be used to predict the adaptations that are displayed in observed morphologies of extant scavengers. Macroscavengers can improve their competitive advantage by detoxifying the toxic defenses of microscavengers; reducing toxicity by one-half, for example, yields an increase in resource consumption: $C = (R - T/2) \times D$, where consumption (C) is a function of the amount of resource available (R), its toxicity (T), and the probability of detection of the carcass by macroscavengers (figure 2a). Alternatively, macroscavengers can develop a strategy by which they increase the probability of detecting the resource, in this model doubling their ability to detect it (figure 2a): $C = (R - T) \times 2D$.

Integrating under the curves provides a means of examining the relative value of each competitive strategy. When the curve is scaled according to the null model, with a relative energy intake of 1.0, toxin production is heavily selected for in microscavengers, reducing relative energy consumption to 0.3. Macroscavenger strategies to overcome chemical defenses are not equivalent, because reducing toxicity by half raises relative consumption to 0.5, but doubling the probability of detection raises relative consumption to 0.7. Thus, this simple, empirically based model predicts that evolutionary pressures of competition from microscavengers will favor macroscavenger adaptations that optimize carcass use by increasing detection probability.

Model predictions, observed scavenger morphology, and supporting evidence

According to my model predictions, the most successful specialized vertebrate macroscavengers should be detection maximizers, and as predicted, the most specialized and obligate vertebrate scavengers have very sensitive olfactory apparatuses and are highly vagile (Stager 1964, Houston 1986); that is, the most successful and most purely obligate vertebrate scav-

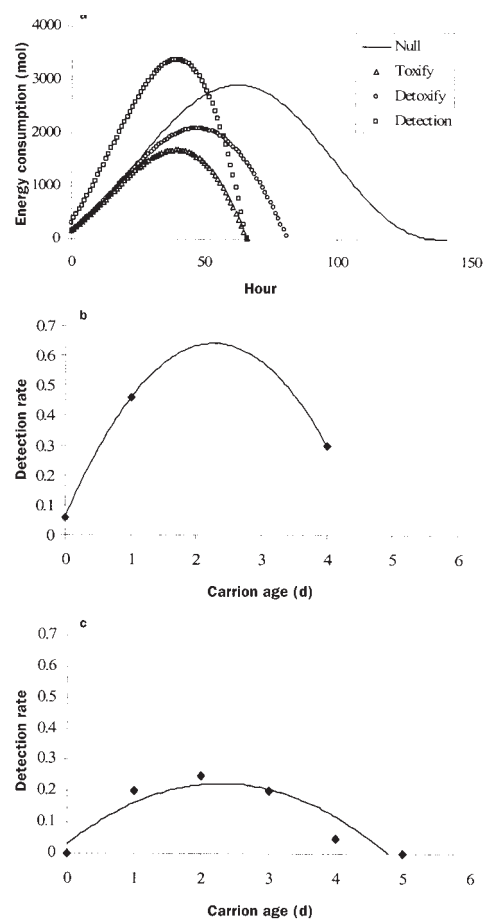


Figure 2. (a) Predictive curves for carcass consumption by macroscavengers. The “null” curve represents the prediction of carcass consumption based on resource availability and probability of detection by macrobiotic scavengers. The “toxify” curve represents consumption incorporating the inclusion of a microbial toxic by-product into the predictive model. The “detoxify” curve represents predicted consumption incorporating a macroscavenger adaptation that produces a twofold decrease in the toxicity of chemical defenses of microscavengers. The “detection” curve represents predicted consumption incorporating a macroscavenger adaptation that produces a twofold increase in carcass detection probability. (b) Observed detection rate of differentially aged carcasses by turkey vultures, *Cathartes aura*, using polynomial smoothing. Data are from Houston 1986. (c) Observed acquisition of carcass resources by the brown tree snake, *Boiga irregularis*, searching for carrion of different ages. Carcasses of varying ages were placed in traps (Shivik 1999) on 14–18 August 1997 proximal to Haputo Beach, Guam. Mice were rotted in a staggered fashion to provide dead mice that were one to five days old on each trap line. Sample sizes were 40 for day zero (empty control trap); 20 for dead mice one, two, three, and five nights old; and 30 for dead mice four nights old. The trend line was drawn using polynomial smoothing.

engers are vultures (Houston 1994). As predicted, the first macroscavenger detection of a carcass is usually by avian species, and consumption is immediate and rapid (figure 2b; Houston 1986). Vultures, which prefer to eat the least rotted food (Houston 1986), find carcasses faster than other vertebrate scavengers (Houston 1986). Furthermore, in independent analyses, Ruxton and Houston (2004) argue that obligate vertebrate scavengers *must* be soaring fliers.

However, decreasing the toxicity of microbes and their by-products is also a useful evolutionary strategy to acquire carcass resources, and the process of selection for improved enzymes may have played a role in the development of specialized salivary secretions in snakes (Savitzky 1980, Kardong 1996, Shivik 1999). The model species I examined, the brown tree snake (*Boiga irregularis*), albeit more widely known for other ecological reasons (Rodda et al. 1997), has a highly specialized oral secretion apparatus (Duvernoy's gland) but paradoxically kills by constricting (Hayes et al. 1993). Because the snake is a voracious scavenger, its oral secretions may have evolved to neutralize the chemical defenses of microscavengers (Shivik and Clark 1997, 1999, Shivik 1999, Jojola-Elverum et al. 2001). Furthermore, brown tree snakes provide an excellent example of carcass detection and consumption that follows the predicted curves and provides support for the parsimonious framework of the models I have outlined. Over time, carrion foraging by the brown tree snake follows a curve predicted by the detoxification strategy (figure 2c). Being far less vagile than other vertebrate species, snakes are expected to develop detoxification strategies to overcome chemical defenses and make the best use of carrion.

There is additional evidence that specialized oral structures in snakes may have evolved under pressures associated with scavenging. Evolutionary pressures are not limited to competition for carcasses, of course, but evolutionarily, as snakes developed from eyeless fossorial species and radiated into terrestrial and arboreal predatory species (Rage 1994), an obligate scavenger evolutionary intermediate was likely. That is, efficient digestion of meat and the need to overcome microscavenger chemical defenses may have influenced the development of specialized salivary enzymes (i.e., venoms) and oral structures (i.e., opisthognathous and protognathous fangs), which could later be behaviorally adapted to subdue live prey (Savitzky 1980). As argued by Huey and colleagues (2003), extant morphology (for carcass consumption) allowed the evolution of new predatory behaviors.

Gans and Elliott (1968) hypothesized that Duvernoy's glands are an imperfect specialization for a current (but perhaps unknown) function. They are still a subject of discussion. Weinstein and Kardong (1994) and Kardong (2002) argued that the biological role of Duvernoy's gland is largely unknown and debatable, but one possible function is to neutralize amphibian toxins; another, I submit, is to neutralize microbes and their toxins. This hypothesis is supported by the fact that so many extant snake species have retained scavenging behaviors (DeVault and Krochmal 2002) and the observation that snake oral secretions inhibit bacterial activity (Thomas

and Pough 1979, Jansen 1983). More detailed experiments are required, such as directly testing the oral secretion of snakes for the inhibition of microbial species as they consume carrion, but the data that are currently available support the possibility of scavenging and oral secretion adaptations for snakes.

Many species—especially invertebrates—that consume carcass resources were not incorporated into the simple models presented here. My models predict that the most efficient carrion-eating insects should be flying, but ambulatory species should evolve other competitive strategies for sequestering the resource. Flies, like birds, are optimized for finding carcasses quickly: Members of Calliphoridae, Sarcophagidae, and Muscidae may find and feed on carcasses within minutes after death (Payne 1965). Other, less vagile species should evolve chemical means of combating microorganisms on carcasses, and some, such as burying beetles (*Nicrophorus* spp.), directly preclude fungal growth on carcasses (Suzuki 2001). A more general trend also considers the metabolic physiology of scavengers. The best scavengers reduce their metabolic rates (through soaring or ectothermy) and thus their caloric requirements, such that consuming food items of lower caloric content might not represent as strong a loss as it would be for other, more metabolically active species.

Competition with microbes for the carrion resource is certainly not the only evolutionary pressure leading to adaptations by snakes, vultures, and other scavengers. Nonetheless, an understanding of the influence and unique aspects of the resource helps to explain (a) why vultures are exceptionally successful within their specialized niche and (b) how a previously unrecognized mechanism helped slow, apodic taxa radiate into predatory species. The models I presented here include testable assumptions (e.g., additive effects of toxins and multiplicative effects of detection probabilities). To develop more explicit models, other details are needed. The amount of the reduction in the caloric content of a carrion item, and the rate at which it declines with time, appear to be unknown; these pieces of information are essential not only for generating a more realistic model but also for establishing the true cost of delayed detection and consumption of carrion. Other mechanisms and influences are undoubtedly at play (e.g., microbial compounds that signal carcass presence also aposematically warn competitors of toxins; commensal bacteriophages and organisms associated with flies may be found in vertebrate scavengers). However, the models described here provide a useful framework for a sensitivity analysis of toxicity, vagility, and detoxification processes relative to competition, and the empirical data presented support these parsimonious models. Specialized structures, be they wings, fangs, or claws, may have developed for improving access to carrion and resulted in current macroscavenger morphologies. Furthermore, given that the adaptations that enabled the use of carrion also enabled the rapid destruction of flesh and the development of specialized predatory behaviors in numerous taxa, the evolutionary and ecological

significance of competition for carrion in ecosystems should not be ignored.

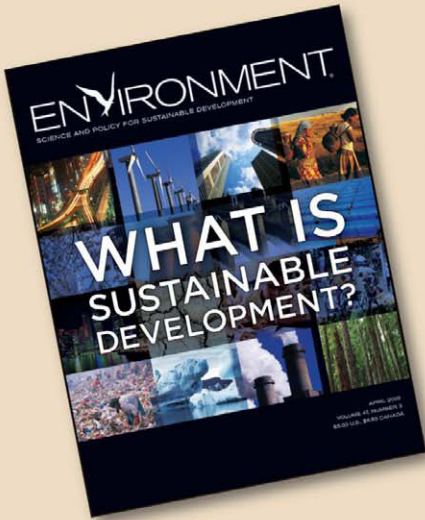
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