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SCAVENGING BY SNAKES: AN EXAMINATION OF THE LITERATURE

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ABSTRACT: Although it is widely known that most species of snakes readily accept carrion in captivity, the notion of scavenging by wild snakes historically has been rejected or ignored. Herein, we review the literature describing instances of scavenging by snakes and consider the implications of carrion use on their ecology. Thirty-nine published accounts yielded 50 observations of scavenging by snakes (43 from field observations and seven from laboratory studies). Thirty-five species from five families were represented, but pitvipers and piscivorous snakes were represented more frequently than other groups. Scavenged material varied widely and included rodents, birds, fish, frogs, and snakes. Olfaction appears to be the overriding sensory modality used for carrion detection. Some species may use scavenging as a deliberate feeding strategy that supplements their regular modes of prey acquisition. Additional knowledge of the scavenging behavior of snakes should provide new insights into the fundamentals of the ecology of snakes.

Key words: Carrion; Diet; Feeding strategies; Scavenging; Snakes

UNDERSTANDING food habits is an integral component of the natural history of all animals. Without thorough knowledge of both diet composition and foraging strategies, we cannot fully understand the resource needs of species, the impact of these species on prey populations, or the flow of energy through food webs (Litvaitis, 2000). Moreover, for many carnivorous vertebrates, our current knowledge of food habits is incomplete due to a lack of information concerning their scavenging behavior (DeVault and Rhodes, 2002; Putman, 1983; Shivik, 1999). For example, scat and stomach content analyses reveal information pertaining to the diet composition of an animal, but usually not to the foraging mode (e.g., whether the food items were preyed upon or scavenged). Many researchers have assumed that most or all items found in the diet of carnivorous vertebrates were preyed upon, and the possibility of scavenging has been ignored unless the food items were too large to have been killed by the study animal (Errington, 1935). However, several studies have demonstrated that most animal carcasses produced in ecosystems are recycled by scavenging rather than by decomposition (Putman, 1983), and, thus, the amount of scavenged material in the diet of many vertebrates probably has been underestimated. Although the scavenging behavior of many vertebrate predators has been overlooked, we believe that research concerning diets of snakes has been particularly hindered by a lack of attention to their scavenging propensity.

Traditionally, carrion foraging by snakes has been discounted or ignored, as apparent from the number of herpetological

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texts that either give no mention of scavenging behavior by snakes or downplay its prevalence (see references in Shivik and Clark, 1997; Zug et al., 2001). This omission exists despite the observations that nearly all snake species readily accept dead prey items in captivity (e.g., Rossi, 1992). Even when snakes are observed scavenging frequently, authors have attributed this behavior to "peculiar conditions" (Capula et al., 1997). Others ascribe scavenging behavior to only certain species: "The North American pit viper (*Agkistrodon piscivorus*), a moccasin with aquatic tendencies, is the only snake that occasionally eats carrion" (Gasc, 1994:114). Cowles and Phelan (1958) and Gillingham and Baker (1981) suggested that rattlesnakes (*Crotalus*) probably forage for carrion frequently, but their hypotheses largely have been overlooked. Only recently have some authors asserted that carrion consumption is an under-appreciated, if not a common, component of snake behavior (Mattison, 1995; Sazima and Strüssmann, 1990; Shivik, 1999; Shivik and Clark, 1997).

Our purposes here are to demonstrate that scavenging behavior in snakes is far more common than previously thought and to stimulate discussion concerning the prevalence and relevance of scavenging as hypothesized by Shivik (1999). To this end, we have summarized published literature of both an observational and an experimental nature.

Review of Published Literature

We used two computerized databases to search for published accounts of scavenging by snakes. We relied primarily on the ISI Web of Science, which includes regional naturalist journals, domestic and foreign herpetological journals, international zoological journals, and museum bulletins. We also used the Wildlife Worldwide database (NISC International, Inc.), an electronic search engine encompassing academic journals, regional publications, dissertations, theses, and government documents.

We supplemented our electronic searches by manually scanning all volumes of *Herpetological Review, Bulletin of the Chicago Herpetological Society, Herpetology* (Southwestern Herpetologist's Society), *The Texas Journal of Science, Journal of the Arizona Academy of Science, The Ohio Naturalist,* and *The Florida Naturalist,* as these journals were not covered by either electronic database. Based on their content, geographic coverage, and intended audience, we felt that these journals would potentially publish accounts of scavenging by snakes.

Our search yielded 32 articles describing carrion use in the field and seven that used laboratory experiments to document scavenging behavior (Table 1). Considering only data from the field, there were 29 direct and unprovoked observations, 8 when the carcass was experimentally introduced, and 6 from stomach content analyses. Twenty-six snake species from five families were represented (Colubridae, n = 12; Viperidae, 11; Acrochordidae, 1; Boidae, 1; Elapidae, 1). Carrion from at least 35 different species of various taxa was scavenged, including fish, rodents, snakes, birds, and a butchered feral hog (*Sus scrofa*; Table 1).

Some groups of snakes were reported scavenging more often than others, although a meaningful statistical analysis of the relative scavenging propensity among groups was not possible due to the lack of sufficient data. For example, a Chi-square test was not appropriate because calculating the null values (the expected rate of scavenging for each group) would require data on the relative number of individuals comprising each group. Of 35 unprovoked scavenging incidents from field observations (observations and stomach content analyses), 11 (31%) were by rattlesnakes (*Crotalus, Sistrurus*) and nine (26%) were by semi-aquatic or aquatic piscivorous snakes. We uncovered numerous accounts of scavenging by snakes that rely primarily on chemosensory information to acquire prey (e.g., *Agkistrodon* and *Thamnophis*; Cock Buning, 1983), documenting the importance of chemical cues in locating carrion (Cowles and Phelan, 1958; Gillingham and Baker, 1981).

Because carrion use is difficult to quantify using traditional diet analysis methods, the fortuitous observations reviewed here must have been unambiguous to the observers. For example, 11 of the 29 field observations (38%) were of snakes scavenging animals that were obviously killed by automobiles. In three observations, snakes were observed peeling squashed frogs or toads from the road surface (Bedford, 1991*a*; Mora, 1999; Resetarits, 1983). Similarly, of the six scavenging events evident from analyses of stomach contents, all of the carrion items were obviously damaged by cars or humans, smelled strongly of decomposition, or contained fly larvae. Because scavengers generally use carcasses of animals that die from starvation, disease, exposure, and other causes that are not easily discerned by casual observation and because carcasses usually are scavenged before advanced decomposition sets in (Putman, 1983), the vast majority of scavenging events by snakes in the field is probably undetectable by current methods.

We acknowledge that there may be an inherent sampling bias associated with compiled data sets because some taxa are more conspicuous and more heavily studied than others. However, the studies reviewed here do suggest that many species will utilize carrion when it is available. Thus, scavenging behavior should be considered in future studies of less conspicuous species.

Discussion

The lack of discussion regarding scavenging by snakes is especially surprising given the number of published accounts pertaining to this phenomenon. However, our purpose here is not to contend that snakes acquire the majority of their food by scavenging (although Wharton, 1966, suggested that cottonmouths, *Agkistrodon piscivorus,* obtain the majority of their food in this manner), but rather to assert that scavenging by snakes is far more common than currently acknowledged. Although a review of this nature does not demonstrate that such behavior is common in all snakes, it does suggest that many species will search out and eat carrion under appropriate conditions, and that some might prefer carrion to live prey (Gillingham and Baker, 1981).

Although many snake species may scavenge only occasionally, some species exhibit certain behaviors that contribute to a high degree of scavenging propensity. Many authors have suggested that pitvipers are most likely among the snakes to exhibit scavenging behavior because their regular "strike and release" mode of prey acquisition dictates that they locate and consume envenomated, dead prey (Cowles and Phelan, 1958; Diller, 1990; Gillingham and Baker, 1981; Lillywhite, 1982; Patten and Banta, 1980; Savitzky, 1992). However, of 35 scavenging events from field observations and stomach content analyses reviewed here, 18 (51%) were by non-venomous species that utilize alternate modes of prey acquisition (Table 1), suggesting that for snakes, scavenging propensity is not governed solely by their modes of prey acquisition.

Sazima and Strüssmann (1990) predicted that several components of snake behavior contribute to scavenging propensity. They postulated that snakes that rely on chemosensory information to acquire prey might forage for carrion more frequently than those whose modes of prey acquisition are driven by visual cues. Additionally, Sazima and Strüssmann (1990) suggested that habitat and diet preferences might be indicators of scavenging propensity because they influence the likelihood of a particular species encountering carrion naturally. Based on these criteria, they predicted that aquatic or semi-aquatic piscivorous snakes would scavenge more frequently than other species. Moreover, Sazima and Strüssmann (1990) suggested that water currents that induce aggregations of carrion heighten the probability of carrion detection by these snakes (see also Savitzky, 1992). Also, chemical gradients may be more uniform and give more dependable directional information in water (Sazima and Strüssmann, 1990).

The papers summarized here support the above hypotheses. Specifically, pitvipers and aquatic or semi-aquatic piscivorous species (species that use chemical cues as the dominant stimuli for prey de-

TABLE 1.—Summary of published research articles and notes citing instances of scavenging by snakes.

Method*	Species	Scavenged material	Citation
Observational	*Acrochordus arafurae*	Eel-tailed catfish (*Hexanematichthys* spp.)	Shine, 1986
	Acrochordus arafurae	Fish ("long tom"; *Strongrylura kreffti*)	Shine, 1986
	Agkistrodon contortrix pictigaster	Cliff swallow (*Petrochelidon pyrrhonota*)	McCrystal and Green, 1986
	Agkistrodon contortrix pictigaster	Texas long-nosed snake (*Rhinocheilus lecontei tessellatus*)	McCrystal and Green, 1986
	Agkistrodon piscivorus conanti	Butchered feral hog (*Sus scrofa*)	Heinrich and Studenroth, 1996
	Agkistrodon piscivorus leucostoma	Snake (*Nerodia* spp.)	Hamel, 1996
	Agkistrodon piscivorus piscivorus	Red-bellied water snake (*Nerodia erythrogaster erythrogaster*)	Berna and Gibbons, 1991
	Alsophis portoricensis richardi	Fish (*Herangula* spp.)	Norton, 1993
	Boiga irregularis	Pale-yellow robin (*Tregallasia capito*)	Torr and Richards, 1996
	Coluber flagellum piceus	Poorwill (*Phaelanoptilus nuttali*)	Cowles, 1946
	Crotalus atrox	Recently-shot squirrel	Kolb, 1946
	Crotalus cerastes laterorepens	Kangaroo rat (*Dipodomys* spp.)	Klauber, 1956
	Crotalus mitchelli pyrrhus	Ground squirrel	Klauber, 1956
	Crotalus viridis	Beechy ground squirrel (*Citellus beechyi*)	Cunningham, 1959
	Crotalus viridis	Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	Ernst, 1992
	Crotalus viridis lutosis	Mountain cottontail (*Sylvilagus nuttalli*)	Diller, 1990
	Epicrates inornatus	Bats (*Erophylla sezekorni*)	Rodriguez-Duran, 1996
	Helicops modestus	Fish (*Geophagus brasiliensis*)	Sazima and Strüssmann, 1990
	Hydrodynastes gigas	Toad (*Bufo parachemis*)	Sazima and Strüssmann, 1990
	Leptodeira annulata	Frog (*Rana vaillanti*)	Mora, 1999
	Liophis miliaris	Frog (*Hyla albomarginata*)	Sazima and Strüssmann, 1990
	Masticophis flagellum	Glossy snake (*Arizona elegans*)	Small et al., 1994
	Nerodia sipedon	Small fish	Raney and Roecker, 1947
	Sistrurus catenatus	Dusty hog-nosed snake (*Heterodon nasicus gloydi*)	Greene and Oliver, 1965
	Sistrurus catenatus	Leopard frog (*Rana pipiens*)	LeRay, 1930
	Thamnophis proximus proximus	Toad (*Bufo americanus* or *Bufo woodhousii*)	Resetarits, 1983
	Thamnophis sirtalis fitchi	Fox sparrow (*Passerella iliaca*)	Feldman and Wilkerson, 2000
	Thamnophis sirtalis sirtalis	Passerine bird	Sajdak and Sajdak, 1999
	Tropidonophis mairii	Various frogs	Bedford, 1991*a*
Stomach contents	*Coluber hippocrepis*	Lizard (*Podarcis sicula*)	Capula et al., 1997
	Coluber hippocrepis	Norway rat (*Rattus norvegicus*)	Capula et al., 1997
	Crotalus adamanteus	Rabbit (*Sylvilagus floridanus*)	Funderburg, 1968
	Crotalus horridus	Rabbit	Swanson, 1952
	Crotalus horridus	Rat	Swanson, 1952
	Pseudechis australis	Flood plain goana (*Varanus panoptes*)	Bedford, 1991*b*
Experimental	*Acrochordus arafurae*	Fish	Shine, 1986
	Boiga irregularis	Mice (*Mus musculus*)	Shivik and Clark, 1997
	Bothrops jararaca	Mouse (*Mus musculus*)	Sazima and Strüssmann, 1990

TABLE 1.—Continued.

Method*	Species	Scavenged material	Citation
	Crotalus horridus	Mouse (*Peromyscus leucopus*)	Nicoletto, 1985
	Crotalus ruber	Desert kangaroo rat (*Dipodomys deserti*)	Patten and Banta, 1980
	Helicops modestus	Fish (*Astyanax scabripinnis*)	Sazima and Strüssmann, 1990
	Helicops modestus	Fish (*Geophagus brasiliensis*)	Sazima and Strüssmann, 1990
	Nerodia sipedon	Fish (*Alosa aestivalis*)	Browder et al., 1995
Laboratory	*Agkistrodon contortrix*	Conspecific	Mitchell, 1977
	Agkistrodon piscivorus	Various fish	Savitzky, 1992
	Crotalus atrox	Mice	Gillingham and Baker, 1981
	Crotalus cerastes	Mouse	Cunningham, 1959
	Crotalus ruber	Meadow mouse (*Microtus californicus*)	Cunningham, 1959
	Crotalus ruber	Mice	Dullemeijer, 1961
	Crotalus spp.	Decomposed white rats	Cowles and Phelan, 1958

* Observational—observation of an unprovoked scavenging event. Stomach contents—snake disgorged a scavenged prey item or a dissected snake contained a scavenged prey item. Experimental—carcass was artificially introduced (e.g., in a trap). Laboratory—captive snake consumed carrion provided by researchers in a controlled setting.

tection) appear to exhibit the highest degree of scavenging propensity. Furthermore, extensive studies on the brown treesnake (*Boiga irregularis*) by Chiszar (1990), Shivik (1998, 1999), Shivik and Clark (1997), and Shivik et al. (2000) provided empirical evidence concerning the importance of chemical cues to scavenging snakes. They demonstrated that brown treesnakes are able to efficiently locate carrion using only olfaction, whereas a combination of visual and chemical cues is needed for them to feed most effectively on live prey. Studies on rattlesnakes have documented the importance of chemical cues to scavenging snakes. Cowles and Phelan (1958) demonstrated that rattlesnakes were attracted to decomposition odors even in the absence of carrion, and Gillingham and Baker (1981) demonstrated that captive western diamondback rattlesnakes (*Crotalus atrox*) easily found and consumed buried, decomposing mice, but not those that were freshly killed. Chemical cues are also the dominant stimuli used by mammals to locate small carrion items (DeVault and Rhodes, 2002).

Does scavenging by snakes represent an opportunistic behavior or a deliberate feeding strategy? Many instances of scavenging by snakes are certainly opportunistic in nature, such as the brown treesnake that searched out and consumed cooked spareribs at a Guam residence (Savidge, 1988). However, several lines of evidence suggest that some species do deliberately search for and consume carrion. Studies pertaining to the importance of chemical cues to scavenging snakes suggest that scavenging via olfaction is a normal strategy of prey acquisition for some species. Furthermore, Savitzky (1992) concluded that scavenging was a deliberate feeding strategy in cottonmouths, based on extensive laboratory observations. Capula et al. (1997) and Shine (1986) suggested that some species adapt to local conditions and actively scavenge when it is profitable, although they generally may not be accustomed to carrion foraging. For certain species, it appears that scavenging has been selected for as an advantageous feeding strategy, supplementing traditional foraging modes.

The benefits of exploiting carrion for its basic energetic content far exceed any associated costs. Carrion provides a food source that can be obtained relatively safely and easily compared to live prey. Additionally, carrion may often be found in predictable places (e.g., roadways) or during predictable times (e.g., after severe weather). Snakes might effectively utilize carrion that more traditionally well adapted scavengers cannot. Speculating on the prevalence of scavenging by snakes, Cowles and Phelan (1958) suggested that for prey species of snakes, "the variety and ubiquity of death from other causes than predation must be very high, sufficiently high to supply abundant food in the secretive kinds of places that snakes should be most capable of investigating and which are inaccessible to avian and large mammalian scavenging competitors." Thus, snakes may occupy a niche that traditionally has been "unassigned" to any other vertebrate taxon (see also Shivik and Clark, 1997). It is also worth noting that this habit of scavenging in inconspicuous places might further contribute to the difficulty in observing scavenging behavior in snakes.

Investigations of ophidian metabolic requirements unveil additional advantages to carrion utilization. Snakes exhibit exceedingly low maintenance metabolisms, and most can survive on a few scant feedings per year (Beaupre and Zaidan, 2001; Beck, 1995; Greene, 1997; Shine, 1986). It is, therefore, possible for snakes to rely largely on infrequent, less energy-rich meals. Carrion, which is by nature ephemeral and unpredictable, may represent such a food source to snakes. Scavenging might allow snakes to meet their low metabolic needs more easily and without the costs associated with subduing prey. Indeed, the commonly held belief that most species do not naturally utilize carrion does not seem to make sense in light of the apparent evolutionary advantages of scavenging (Shivik 1999).

The frequency and propensity with which snakes scavenge necessitate a change in perceptions of ophidian feeding and natural history. The potential importance of this phenomenon should not be overlooked; carrion use by snakes might substantially influence their fitness. Quantification of this phenomenon through laboratory and field research would elucidate the frequency and significance of carrion use among snakes and quite possibly provide new insights into the ecology of many species.

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