

Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers

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Abstract: Vertebrate scavengers and decomposers compete for animal carcasses in all temperate and tropical ecosystems. We examined the influence of carcass size, forest type, and air temperature on the fate of rodent carcasses at the Savannah River Site, South Carolina, USA. Three hundred rodent carcasses were placed at random locations in forested habitats and scavengers were identified using remote photography. Seventeen species of vertebrates removed 104 of 300 (35%) rodent carcasses over a year. Raccoons (*Procyon lotor* (Linnaeus, 1758)) and Virginia opossums (*Didelphis virginiana* Kerr, 1792) scavenged most frequently. For scavenged carcasses, the mean time to carcass removal was 2.58 days after placement. Carcass acquisition by scavengers and decomposers was influenced moderately by forest type and carcass size, although ambient air temperature considerably influenced the fate of carcasses. Vertebrates removed fewer carcasses as temperatures increased: only 28 of 144 (19%) carcasses were scavenged when temperatures exceeded 17 °C. The temporal pattern of carcass removal by vertebrates, however, did not vary with temperature. Consistent rates of carcass removal by vertebrates across the year and increased activity by insects during warm weather led to elevated levels of decomposition during summer months. This study confirms the complexity and dynamic nature of competitive relationships among scavengers and decomposers.

Résumé : Les vertébrés charognards font compétition aux décomposeurs pour l'utilisation des carcasses dans tous les écosystèmes tempérés et tropicaux. Nous avons examiné l'effet de la taille de la carcasse, du type de couvert forestier et de la température de l'air sur le sort de carcasses de rongeurs dans le site de la rivière Savannah, Caroline du Sud, É.-U. Nous avons placé 300 carcasses de rongeurs à des sites choisis aléatoirement dans des habitats forestiers et identifié les charognards par photographie à distance. Au cours d'une année, 17 espèces de vertébrés ont retiré 104 (35 %) des 300 carcasses de rongeurs. Les rats laveurs (*Procyon lotor* (Linnaeus, 1758)) et les opossums d'Amérique (*Didelphis virginiana* Kerr, 1792) sont les charognards les plus communs. Le temps écoulé en moyenne avant le retrait d'une carcasse est de 2,58 jours après sa mise en place. Il n'existe qu'une faible relation entre l'acquisition des carcasses par les charognards et les décomposeurs et le type de couvert forestier et la taille de la carcasse; cependant, la température de l'air ambiant affecte considérablement le sort des carcasses. Les vertébrés retirent de moins en moins de carcasses à mesure que les températures s'élèvent: seulement 28 (19 %) de 144 carcasses ont été utilisées par les charognards aux températures supérieures à 17 °C. Cependant, le pattern temporel annuel de retrait des carcasses par les vertébrés ne varie pas avec la température. Des taux soutenus de retrait des carcasses par les vertébrés au cours de l'année, associés à une activité accrue des insectes durant les périodes chaudes, expliquent les niveaux plus élevés de décomposition durant les mois d'été. Note étude confirme la complexité et le dynamisme des relations de compétition entre les charognards et les décomposeurs.

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Introduction

The fate of carrion in terrestrial ecosystems is potentially a key area of ecological study. The importance of carrion is derived, in part, from the magnitude of animal carcasses produced in many ecosystems (Houston 1979; Putman 1983; DeVault et al. 2003). Carrion may be consumed by a wide variety of organisms, particularly carnivorous vertebrates, insects, and microbes. However, few studies have examined

the proportion of carcasses consumed by specific taxa or the factors influencing the allocation of carrion resources in terrestrial ecosystems. Our understanding of energy flow pathways in terrestrial ecosystems would be greatly enhanced by more detailed investigations of the relative roles of scavengers and decomposers in recycling animal carcasses (DeVault et al. 2003). Furthermore, perceptions of food habits and feeding strategies of many vertebrates could be refined with additional knowledge of the role that facultative

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scavenging plays in their daily energy budgets (DeVault and Krochmal 2002).

Animal carcasses usually are consumed soon after death, except in very cold climates. The proportion of carcasses that are scavenged by vertebrates as opposed to those that undergo decomposition is governed by competitive relationships among the organisms that attempt to sequester the resource. The most successful vertebrate scavengers are those that are able to detect and consume carrion rapidly (Houston 1979; Shivik 1999). A summary of studies using experimental carrion baits to measure scavenging efficiency showed that across all climates and localities, vertebrates consumed 75% of available carcasses (DeVault et al. 2003). Further, recent empirical studies using remote photography have demonstrated that many vertebrate species readily use carrion resources (Kostecke et al. 2001; Peterson et al. 2001; Bumann and Stauffer 2002; DeVault and Rhodes 2002). However, the competitive balance among scavengers and decomposers varies tremendously across ecosystem types and climate regimes (DeVault et al. 2003). More locally, competition for carrion may be influenced by air temperature, habitat type, and carcass size (Putman 1983; DeVault and Rhodes 2002).

Decomposers compete with vertebrates in a variety of ways. The abundance and ubiquity of insects allows them to exploit carcasses rapidly after an animal dies. For instance, flies of the families Calliphoridae, Sarcophagidae, and Muscidae often feed and lay eggs upon fresh carcasses within a few minutes of death (Payne 1965). Ants and beetles also are major consumers of carrion (Payne 1965). Microbes compete for carrion by producing toxins (i.e., botulin toxin) that are dangerous to most vertebrates (Janzen 1977). Microbes advertise their toxicity with various amines and sulfur compounds, which at high concentrations repel vertebrate scavengers. At low concentrations, however, the microbial products of decomposition may attract vertebrates to edible carrion (DeVault et al. 2003).

Relationships among decomposers are more intricate than those with vertebrate scavengers. For example, insects and bacteria may benefit mutually when feeding on carrion. Fly larvae aerate carcasses, allowing aerobic microbes to penetrate deep into animal tissues, and fly larvae liquefy muscle tissue as they feed, providing a high-quality environment for microbes (Putman 1983). Even at summertime temperatures, carcasses experimentally kept free from insects mummify before microbes fully decompose them (Payne 1965; Putman 1978a). Further, Janzen (1977) speculated that flies are important distributors of carrion bacteria. At high concentrations, the toxins produced by microbes repel vertebrate scavengers, possibly allowing insects to consume carcasses inedible to vertebrates. Unfortunately, little information is available concerning the effects of microbial toxins on insects.

The elucidation of factors that influence the acquisition of small carrion items by vertebrates, insects, and microbes is the focus of this study. We use the term "scavenger" for vertebrates, as they are able to remove large portions of carrion individually in a short period of time. "Decomposers" are insects and microbes, which individually consume only small portions of a carcass. In a preliminary study (DeVault and Rhodes 2002), rodent carrion bait attracted a variety of ver-

tebrate scavengers (11 species identified), which removed 65% of the carcasses placed in forested habitats during the winter within 14 days. DeVault and Rhodes (2002) determined that the number of carcasses removed by vertebrates was strongly correlated (positively) with ambient air temperature during cool weather. Here, we extend that preliminary work to span an entire year, allowing investigation of how habitat type, carcass size, and temperature influence the acquisition of small carrion items across seasons. Because past research suggests that vertebrates consume most available carrion (DeVault et al. 2003), we focus on species identification only for vertebrates, using remote cameras and carrion bait. We also extend the analyses to include questions concerning carrion acquisition within the vertebrate community.

Methods

Study site and selection of experimental points

This study was conducted at the 78 000 ha Savannah River Site (SRS), a nuclear facility owned and operated by the United States Department of Energy near Aiken, South Carolina, USA. Approximately 64% of the SRS is covered in loblolly pine (*Pinus taeda* L.), longleaf pine (*Pinus palustris* P. Mill.), and slash pine (*Pinus elliottii* Engelm.), which is managed for timber. An additional 15% of the land cover is classified as bottomland hardwood (Workman and McLeod 1990). The average annual rainfall at the SRS is 120 cm, and the average temperatures in winter and summer are 9 and 26 °C, respectively (White and Gaines 2000).

A subset of the forested habitat on the SRS that was free from management activities (timber harvest and controlled burns) was used for study. Thirty-eight timber compartments and all "set-asides" (research areas that are permanently free from management activities), encompassing approximately 30 870 ha, were delineated from a 1999 digital habitat map (Wiggins-Brown et al. 2000) using Geographic Information System (GIS) software (ArcView 3.2, Environmental Systems Research Institute, Inc.). All upland pine and bottomland hardwood habitat categories were condensed into two distinct habitat classes representing the two forest types. We used the Animal Movement extension (Hooe and Eichenlaub 1997) in ArcView 3.2 to generate 150 geographically random point locations within each of the two habitat classes. These points served as experimental locations (Universal Transverse Mercator coordinates) for carcass placement.

Field methods

Rodent carcasses were placed at each of the 300 random points during 25, 13-day time periods (rounds) from 7 December 2001 through 27 November 2002. One idle day followed each round. Rounds were continuous, except one week between rounds 1 and 2 was left idle because of snow. During each round, the influence of habitat type and carcass size on the probability of carcass removal by vertebrates was examined using a factorial experimental design. Habitat type was defined using the two GIS-derived habitat classes described above (upland pine and bottomland hardwood). Carcass size was categorical: mice (*Mus musculus* Linnaeus, 1758) averaged 19.4 g (SD = 1.7) and rats (*Rattus*

Table 1. Numbers of brown-furred house mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*) removed by vertebrate scavengers and identified by remote photography.

Class	Species	Mice	Rats	Total
Mammalia	Raccoon (<i>Procyon lotor</i>)	15	16	31
	Virginia opossum (<i>Didelphis virginiana</i>)	12	17	29
	Feral pig (<i>Sus scrofa</i>)	4	5	9
	Gray fox (<i>Urocyon cinereoargenteus</i>)	0	4	4
	Cotton mouse (<i>Peromyscus gossypinus</i>)	2	0	2
	Southern flying squirrel (<i>Glaucomys volans</i>)	1	1	2
	Striped skunk (<i>Mephitis mephitis</i>)	1	0	1
	Reptilia	Black racer (<i>Coluber constrictor</i>)	3	2
	Eastern box turtle (<i>Terrapene carolina</i>)	1	1	2
	Copperhead (<i>Agkistrodon contortrix</i>)	0	1	1
	Rat snake (<i>Elaphe obsoleta</i>)	0	1	1
	Canebrake rattlesnake (<i>Crotalus horridus atricaudatus</i>)	1	0	1
Aves	American crow (<i>Corvus brachyrhynchos</i>)	0	3	3
	Red-shouldered hawk (<i>Buteo lineatus</i>)	0	2	2
	Black vulture (<i>Coragyps atratus</i>)	0	1	1
	Red-tailed hawk (<i>Buteo jamaicensis</i>)	0	1	1
	Turkey vulture (<i>Cathartes aura</i>)	0	1	1
Unknown		5	3	8
Total		45	59	104

Results

In total, vertebrates removed 104 of 300 (35%) rodent carcasses (Table 1). Seventy-six of the 156 (49%) carcasses placed during cool-weather rounds were scavenged by vertebrates; of the remaining 80 carcasses, 36 (45%) still contained some apparently edible biomass at the end of the rounds. During warm-weather rounds, vertebrates removed only 28 of 144 (19%) carcasses. All of the remaining carcasses had completely decomposed (leaving only a few scattered bones and pieces of skin) by the end of the rounds, and usually before 2 days had elapsed.

Raccoons (*Procyon lotor* (Linnaeus, 1758)) and Virginia opossums (*Didelphis virginiana* Kerr, 1792) accounted for 60 (58%) of the scavenged carcasses. The remaining 44 carcasses were removed by 15 other species (Table 1). Eleven of these species scavenged only one or two carcasses. We were unable to identify the species responsible for carcass removal in eight cases because of camera system failure. For five of these cases, we also were unable to measure elapsed time to carcass removal.

Carcass size and habitat type both seemed to influence competition among vertebrates and decomposers for carcasses. Vertebrates removed 45 mice and 59 rats (Table 1). Forty carcasses were removed in upland pine habitats, whereas 64 were removed in bottomland hardwood habitats. The difference between habitats, however, was attributable to the top three scavenger species. Raccoons, Virginia opossums, and feral pigs (*Sus scrofa* Linnaeus, 1758) removed 45 carcasses in bottomland hardwood habitats, but only 24 carcasses in upland pine habitats. The remaining 14 vertebrate species removed 14 carcasses in bottomland hardwoods and 13 carcasses in upland pines.

In logistic regression analysis, the top seven models were similar regarding the percentage of cases correctly classified and the AIC values (all Δ AIC < 2.6; Table 2). These models

all included the variables temperature and habitat. Temperature was the most important variable in the top seven models: Wald χ^2 values ranged from 12.50 to 28.69, all with corresponding *P* values < 0.001. After the top seven models, model fit declined sharply for the other possible models (all Δ AIC > 7.6). The influence of ambient air temperature during the first week of a round on the number of carcasses removed during the round was highly significant, with fewer carcasses removed by vertebrates as temperature increased (Fig. 1).

Across all rounds, mean time to carcass removal was 2.58 days (range = 0.13–11.93, SD = 2.80, *n* = 99). However, the mean time to carcass removal differed substantially between cool-weather and warm-weather rounds (Fig. 2). During cool-weather rounds the mean time to carcass removal was 3.13 days (range = 0.13–11.93, SD = 3.02, *n* = 74), whereas during warm-weather rounds the mean was only 0.94 days (range = 0.20–4.13, SD = 0.87, *n* = 25). Of the 28 carcasses that vertebrates removed during warm-weather rounds, however, only 4 were removed after 1.5 days had elapsed. Within 1.5 days of carcass placement (when few carcasses had completely decomposed), the mean time to carcass removal during cool-weather and warm-weather rounds was similar (cool-weather mean = 0.72, SD = 0.46, *n* = 28; warm-weather mean = 0.69, SD = 0.41, *n* = 21).

Discussion

The relative number of scavenging events attributed to various vertebrate species resembled the relative abundance of carnivorous species at the SRS, with a few exceptions. The top three mammal species (raccoon, Virginia opossum, and feral pig) are very common at the SRS (Cothran et al. 1991), and the top reptile species (black racer, *Coluber constrictor* Linnaeus, 1758) is one of the most abundant snakes

Table 2. Best-fit logistic models of small carcass removal by vertebrate scavengers.

Model	Δ AIC	% Correct	Variable	Coefficient	SE
1	0.000	69.0	Intercept	-1.79	0.41
			TEMP	0.10	0.02
			HAB	0.81	0.27
			SIZE	0.48	0.26
2	0.727	70.0	Intercept	-1.93	0.43
			TEMP	0.10	0.02
			HAB	1.09	0.37
			SIZE	0.75	0.36
3	1.189	69.3	HAB \times SIZE	-0.59	0.53
			Intercept	-2.07	0.53
			TEMP	0.12	0.03
			HAB	1.40	0.71
4	1.239	69.3	SIZE	0.50	0.26
			TEMP \times HAB	-0.03	0.04
			Intercept	-1.97	0.47
			TEMP	0.11	0.02
5	1.322	70.7	HAB	1.00	0.35
			SIZE	0.65	0.33
			TEMP \times HAB \times SIZE	-0.02	0.03
			Intercept	-1.53	0.38
6	1.592	69.0	TEMP	0.10	0.02
			HAB	0.80	0.26
			Intercept	-1.59	0.51
			TEMP	0.09	0.03
7	2.531	70.7	HAB	0.81	0.27
			SIZE	0.06	0.70
			TEMP \times SIZE	0.02	0.04
			Intercept	-1.81	0.50
			TEMP	0.12	0.03
			HAB	1.38	0.70
			TEMP \times HAB	-0.03	0.04

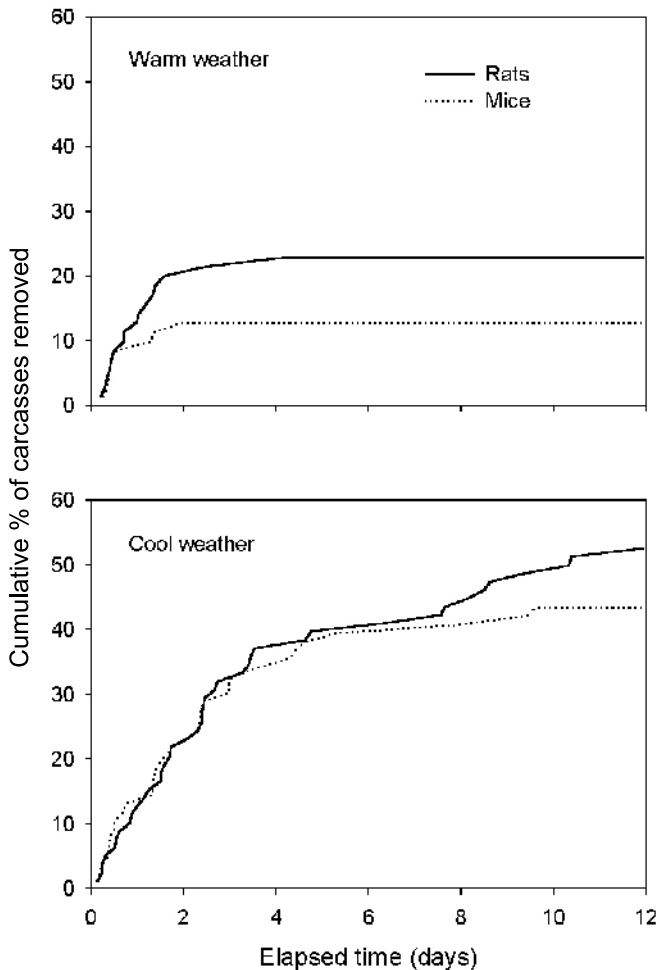
Note: % Correct indicates the number of carcasses (cases) correctly predicted by the logistic model as removed or not removed by vertebrates. TEMP is the mean ambient air temperature ($^{\circ}$ C) during the first week of the round in which a case was included. HAB and SIZE are treated as categorical variables: HAB is the habitat in which the carcass was placed (0 = bottomland hardwood; 1 = upland pine); SIZE is the size of the carcass (0 = rat; 1 = mouse). All models were significant at $P < 0.001$ as evaluated by the model χ^2 .

throughout the site (J.W. Gibbons, personal communication). All of the bird species that scavenged carcasses are common year-round residents at the SRS (Potter et al. 1980). Some species, however, were recorded surprisingly few times, or were completely absent from our study. Eastern coyotes (*Canis latrans* Say, 1823) and eastern gray squirrels (*Sciurus carolinensis* Gmelin, 1788), recorded twice each during the preliminary study (DeVault and Rhodes 2002), and bobcats (*Lynx rufus* (Schreber, 1777)), recorded once, were notably absent from the current study. Also, gray foxes (*Urocyon cinereoargenteus* (Schreber, 1775)) removed relatively few carcasses in relation to their abundance at the SRS (Cothran et al. 1991). We speculate that eastern coyotes and bobcats might have been more sensitive to human scent left at camera stations than raccoons, Virginia opossums, and feral pigs. The dominance of mammals over birds in removing carcasses likely resulted from the more acute olfactory senses of the former. Decomposition odor is the dominant stimulus used by mammals (Henry 1977; DeVault and Rhodes 2002) and snakes (Gillingham and Baker 1981; Shivik and Clark 1997; DeVault and Krochmal 2002) to locate carrion. Although reptiles are inactive during cold

weather, they collectively removed more carcasses (10) than the birds (8) over the entire year (Table 1). It appears that, in general, small carcasses (i.e., rodents) are more likely to be scavenged by mammals and reptiles, which use olfactory cues to locate carrion. Birds such as raptors and vultures are more successful at locating larger carcasses and those in structurally open habitats, where visual acuity is more effective (Peterson et al. 2001; DeVault et al. 2003). Surprisingly, only one turkey vulture (*Cathartes aura* (Linnaeus, 1758)), a species common at the SRS and known to possess a highly developed olfactory sense (Stager 1964), removed a carcass (Table 1).

Although a variety of vertebrates scavenged small carcasses in this study, the overall competitive balance for small carrion items was shifted toward the decomposers at the SRS. Collectively, vertebrates removed fewer carcasses (35%) in this study than in most others using small carrion bait (DeVault et al. 2003). The warm climate in South Carolina and the local abundance of insects undoubtedly contributed to the success of the decomposers. Where carcasses are completely free from insects in the winter, scavenging efficiency by vertebrates on small carrion items

Fig. 2. Cumulative percentage of carcasses removed as a function of time during warm weather (temperature range during first week, 22.6–27.8 °C; $n = 12$ rounds, 144 carcasses) and cool weather (temperature range during first week, 5.8–17.0 °C; $n = 13$ rounds, 156 carcasses). The elapsed time was unknown for five scavenging events; these were deleted from the analysis.



approaches 100% (Mullen and Pitelka 1972; Putman 1983). At the SRS, insects (i.e., flies and ants) are usually somewhat active even in winter.

The similar model fit of logistic equations incorporating various combinations of predictor variables suggests that all factors (air temperature, carcass size, habitat type) played a role in mediating competition among scavengers and decomposers, although air temperature was the most important. Temperature influences the speed of decomposition by insects and bacteria (Putman 1978a; Shean et al. 1993) and thus limits the temporal availability of carcasses to vertebrates. However, air temperature did not greatly affect the rate of carcass removal by vertebrates.

For example, during both warm- and cool-weather rounds, the pattern of carcass removal by vertebrates over time was similar for rats and mice until the mice completely decomposed (1 day during warm weather, 8 days during cool weather; Fig. 2). Likewise, for both rats and mice, the rate of carcass removal by vertebrates was similar across temperature regimes until decomposition occurred in warm weather.

At 2 days after carcass placement, vertebrates had removed about 20% of the rats during both warm- and cool-weather rounds (Fig. 2). Similarly, vertebrates removed about 10% of the mice during both warm- and cool-weather rounds after 1 day (Fig. 2). Thus, the temporal pattern of carcass removal by vertebrates was roughly equal across temperature regimes and carcass sizes until complete decomposition occurred (see also Putman 1983).

Given that decomposition odor is the chief cue used by vertebrates to locate carrion, similar rates of scavenging pressure across carcass sizes and temperatures suggest that the magnitude of decomposition odor varied little with respect to carcass size and temperature. Regarding carcass size, the most obvious explanation is that the two carcass sizes used in this study did not differ enough to substantially influence the magnitude of odor, although we did not test this hypothesis. Considering temperature, data from Putman (1978a) support our supposition that decomposition odor varied little across temperatures. Putman (1978a) reported similar low rates of CO₂ production (a measure of decomposer activity) in both cold and warm weather for up to 5 days after carcass placement. Only after fly larvae hatched and began tunneling through the carcasses during warm weather did CO₂ production increase above winter levels. In the absence of insect activity, aerobic microbes apparently are confined to the surface of carcasses for several days, limiting their progress in decomposition.

Because we did not measure decomposer activity directly, it is difficult to determine the relative contributions of insects and microbes in decomposing the carcasses not removed by vertebrates. However, available data suggest that insects (primarily fly larvae) can consume small carcasses very rapidly because of the high surface:volume ratio of such carrion. For example, at a study site located only 200 km from the SRS, 1000–1400 g baby pig carcasses were reduced to about 10% of their original mass only 2 days after fly larvae hatched and began feeding (Payne 1965). In a similar study, fly larvae consumed over 80% of all the decomposed material in mouse carcasses (18–28 g) protected from vertebrates in summer and autumn (Putman 1978b). We likewise believe that fly larvae were the major decomposers of small mammal carrion in the current study. Fly larvae were visible, sometimes in great masses, in several photographs of decomposed carcasses. Also, the time frame of ceased scavenging activity by vertebrates during warm weather (approximately 2 days; Fig. 2) corresponded to the time required for fly larvae to fully consume carcasses of this size (Payne 1965; Putman 1978a). Microbes are apparently more successful at decomposing larger carcasses. For example, during a period of large-scale mortality of African elephants (*Loxodonta africana* (Blumenbach, 1797)), bacteria decomposed 95%–97% of the soft tissues of elephant carcasses; insect larvae consumed the remaining 3%–5% (Coe 1978).

One intriguing question concerns the opposite trends observed in the relationship between mean air temperature and scavenging efficiency by vertebrates reported in this study and by DeVault and Rhodes (2002). In the winter of 2000–2001, vertebrates removed more carcasses per round as temperature increased (DeVault and Rhodes 2002), whereas during cool weather in the current study, the opposite trend

was observed (Fig. 1). In addition, during the DeVault and Rhodes (2002) study, the mean time to carcass removal by vertebrates was 5.6 days, and 50% of the scavenged carcasses were removed after 6 days had elapsed from the time of carcass placement. Conversely, during cool weather in the current study, the mean time to carcass removal was 3.13 days and vertebrates removed only 17% of scavenged carcasses after 6 days. A difference in seasonal temperatures between the two studies was most likely one factor contributing to both of the observed discrepancies.

Although microbial activity is limited during cold weather, low levels are positively correlated with temperature (Putman 1978a), thus influencing odor production and vertebrate scavenging efficiency. The mean air temperature in the winter of 2000–2001 was 2 °C lower than the average winter temperature at the SRS (9 °C; White and Gaines 2000), whereas in the current study the mean winter temperature was 1 °C higher than average. Differences in seasonal temperature between years may have affected the dynamics of the insect community, leaving primarily the low level of microbial activity to control odor production and decomposition in the colder winter studied by DeVault and Rhodes (2002). In the absence of significant insect activity, vertebrates were able to remove carcasses for up to 14 days after carcass placement, and their success in removing carcasses was correlated positively to temperature and thus microbial activity (DeVault and Rhodes 2002). In the current study, insects were active all winter and consumed many carcasses before vertebrates could locate them by olfaction. Thus, the interplay between microbial and insect activity and, by extension, scavenging efficiency by vertebrates seems to be governed by seasonal temperatures.

A variety of factors mediates the acquisition and consumption of carrion resources, and the inherent intricacy of the interplay among these factors influences both the rate of energy sequestration and the path of energy flow in terrestrial ecosystems. Our data indicate that the availability of carrion resources to vertebrates in this southern climate is strongly affected by temperature, primarily through its influence on the activity of insects and thus on the colonization of carcasses by microbes. In turn, competition for available carrion among vertebrates is influenced by carcass size, as a consequence of both the rate at which the resource can be exploited by decomposers and the visual conspicuousness of the carcass. The general agreement between estimates of carnivore abundance in the two habitats and the proportions of carcasses utilized by the various species in those habitats strongly reinforces the idea that most species will utilize carrion resources when they are detected. The results of this study point to the need for additional experimental investigations that can further elucidate the energy flow pathways of carrion resources through terrestrial food webs and clarify the role of temperature as a factor that mediates the acquisition of carrion resources among insects, microbes, and vertebrates.

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References

- Bumann, G.B., and Stauffer, D.F. 2002. Scavenging of ruffed grouse in the Appalachians: influences and implications. *Wildl. Soc. Bull.* **30**: 853–860.
- Burnham, K.P., and Anderson, D. 2002. Model selection and multi-model inference. Springer-Verlag, New York.
- Coe, M. 1978. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. *J. Arid Environ.* **1**: 71–86.
- Cothran, G.E., Smith, M.H., Wolff, J.O., and Gentry, J.B. 1991. Mammals of the Savannah River Site. SRO-NERP-21. Savannah River Ecology Laboratory, Aiken, S.C.
- Danielson, W.R., Degraaf, R.M., and Fuller, T.K. 1996. An inexpensive compact automatic camera system for wildlife research. *J. Field Ornithol.* **67**: 414–421.
- DeVault, T.L., and Krochmal, A.R. 2002. Scavenging by snakes: an examination of the literature. *Herpetologica*, **58**: 429–436.
- DeVault, T.L., and Rhodes, O.E., Jr. 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. *Acta Theriol.* **47**: 185–192.
- DeVault, T.L., Rhodes, O.E., Jr., and Shivik, J.A. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**: 225–234.
- Gillingham, J., and Baker, R. 1981. Evidence for scavenging behavior in the western diamondback rattlesnake (*Crotalus atrox*). *Z. Tierpsychol.* **55**: 217–227.
- Henry, J.D. 1977. The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). *Behaviour*, **61**: 82–105.
- Hooge, P.N., and Eichenlaub, B. 1997. Animal movement extension to ArcView. Version 1.1. Alaska Science Center — Biological Science Office, US Geological Survey, Anchorage, Alaska.
- Hosmer, D.W., and Lemeshow, S. 1989. Applied logistic regression. Wiley and Sons, New York.
- Houston, D.C. 1979. The adaptations of scavengers. *In* Serengeti, dynamics of an ecosystem. *Edited by* A.R.E. Sinclair and M.N. Griffiths. University of Chicago Press, Chicago. pp. 263–286.
- Janzen, D.H. 1977. Why fruits rot, seeds mold, and meat spoils. *Am. Nat.* **111**: 691–713.
- Kostecke, R.M., Linz, G.M., and Bleier, W.J. 2001. Survival of avian carcasses and photographic evidence of predators and scavengers. *J. Field Ornithol.* **72**: 439–447.
- Mullen, D.A., and Pitelka, F.A. 1972. Efficiency of winter scavengers in the Arctic. *Arctic*, **25**: 225–231.
- Norusis, M.J. 1999. SPSS regression models 10.0. SPSS Inc., Chicago.
- Payne, J.A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology*, **46**: 592–602.
- Peterson, C.A., Lee, S.L., and Elliott, J.E. 2001. Scavenging of waterfowl carcasses by birds in agricultural fields of British Columbia. *J. Field Ornithol.* **72**: 150–159.
- Potter, E.F., Parnell, J.F., and Teulings, R.P. 1980. Birds of the Carolinas. University of North Carolina Press, Chapel Hill, N.C.

- Putman, R.J. 1978a. Patterns of carbon dioxide evolution from decaying carrion. Decomposition of small mammal carrion in temperate systems 1. *Oikos*, **31**: 47–57.
- Putman, R.J. 1978b. Flow of energy and organic matter from a carcass during decomposition. Decomposition of small mammal carrion in temperate systems 2. *Oikos*, **31**: 58–68.
- Putman, R.J. 1983. Carrion and dung: the decomposition of animal wastes. Edward Arnold, London.
- Shean, B.S., Messinger, L., and Papworth, M. 1993. Observations of differential decomposition on sun exposed v. shaded pig carrion in coastal Washington State. *J. Forensic Sci.* **38**: 938–949.
- Shivik, J.A. 1999. Carrion, context, and lure development: the relative importance of sensory modalities to foraging brown treesnakes (*Boiga irregularis*). Ph.D. thesis, Colorado State University, Fort Collins, Colo.
- Shivik, J.A., and Clark, L. 1997. Carrion seeking in brown tree snakes: importance of olfactory and visual cues. *J. Exp. Zool.* **179**: 549–553.
- SPSS Inc. 1999. SPSS base 10.0 applications guide. SPSS Inc., Chicago.
- Stager, K.E. 1964. The role of olfaction in food location by the Turkey Vulture (*Cathartes aura*). Los Angel. Cty. Mus. Contrib. Sci. No. 81.
- White, D.L., and Gaines, K. F. 2000. The Savannah River Site: site description, land use, and management history. *Stud. Avian Biol.* **21**: 8–17.
- Wiggins-Brown, H., Pinder, J.E., III, Guy, K.K., and Rea, T.E. 2000. 1999 habitat map of the Savannah River Site. Savannah River Ecology Laboratory, Aiken, S.C.
- Workman, S.K., and McLeod, K.W. 1990. Vegetation of the Savannah River Site: major community types. SRO-NERP-19. Savannah River Ecology Laboratory, Aiken, S.C.