Identification of vertebrate scavengers of small mammal carcasses in a forested landscape

Travis L. DeVAULT* and Olin E. RHODES Jr

DeVault T. L. and Rhodes O. E. Jr 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. Acta Theriologica 47: 185–192.

We identified vertebrate scavengers of small mammal carcasses at the 780-km^2 Savannah River Site during the winter of 2000–2001. Rodent carcasses, differing in size and visual conspicuousness, were placed in upland pine forests and bottomland hardwood forests during six 2-week periods. Sixty-two of the 96 carcasses (65%) were removed by vertebrates. With the aid of remote photography, we identified 11 species of scavengers removing carcasses. Raccoons *Procyon lotor*, gray foxes *Urocyon cinereoargenteus*, and feral pigs *Sus scrofa* scavenged most frequently. The mean elapsed time for carcass removal was 5.6 days. The number of carcasses removed by vertebrates did not differ significantly with respect to carcass size, visual conspicuousness, or habitat type; however, air temperature was strongly correlated (positively) with carcass removal. Our study demonstrates that many mammal species are capable of utilizing small carrion items as a food resource, and suggests that scavenging may account for a higher proportion of the diet of some facultative scavengers than is now widely assumed.

Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907, USA

Key words: carrion, diet, food habits, remote photography, scavenging

Introduction

Most vertebrate carnivores should be considered facultative scavengers due to their opportunistic nature. Although carrion consumption may expose potential scavengers to risks that predation does not, such as disease (Janzen 1977), conflicts with other scavengers (Wallace and Temple 1987, Halley and Gjershaug 1998), and exposure to predation (McKillup and McKillup 1994, Jones 1998), the benefits of scavenging over predation may offset these risks. By scavenging, the possibility of injury from a prey animal is eliminated, and no energy is lost from chasing and subduing the prey animal. Consequently, most vertebrate carnivores take advantage of carrion when it is available (Houston 1979, Wilton 1986), and some of the more well-adapted facultative scavengers, such as red foxes *Vulpes vulpes* (Henry 1977) and spotted hyenas *Crocuta crocuta* (Cooper *et al*. 1999) apparently abandon predation and scavenge exclusively in some circumstances.

*Current address: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802, USA, e-mail: devault@srel.edu

Small carrion items, particularly rodent carcasses, may provide an especially valuable food resource for some vertebrates. Several authors indicate that an appreciable number of small carcasses are likely available to vertebrate scavengers (Cowles and Phelan 1958, Bobek 1969, 1973, Putman 1976). Additionally, when compared to larger carcasses, utilization of small carcasses minimizes competition from other scavengers and thus lowers the risk of predation associated with scavenging. However, the actual extent of small carrion items in the diet of vertebrate carnivores is difficult to quantify, primarily due to the difficulties in detection of such items using standard carnivore diet analysis techniques (scat and stomach content analysis). Thus, the importance of small carrion items in the diet of many vertebrate carnivores is likely under-appreciated (Putman 1976).

The ratio of small carcasses that are scavenged by vertebrates to those that simply decompose appears to vary with season and habitat type, although comparative data are largely lacking. Similarly, facultative scavenger species probably vary in scavenging propensity, depending on foraging strategies, sensory abilities, and evolutionary histories. However, few studies have investigated which vertebrate species are most likely to scavenge small carcasses, or the manner in which various environmental conditions influence this phenomenon. Mullen and Pitelka (1972), Putman (1976), and Simonetti *et al*. (1984) investigated scavenging efficiency of small carrion items with experimentally-placed rodent carcasses during winter. They reported scavenging rates of 99 to 100%. Using tracks in the snow, Mullen and Pitelka (1972) attributed most of their scavenging events to arctic foxes *Alopex lagopus* and red foxes. Putman (1976) also attributed scavenging events primarily to red foxes, whereas Simonetti *et al*. (1984) credited "local predators" with carcass removal, primarily a didelphid *Marmosa elegans*, although neither described how they arrived at these conclusions.

Vertebrate scavengers compete with microbes and arthropods for carrion, especially during periods of warm weather (Janzen 1977). Although Putman (1976) reported seasonal variation in scavenging efficiency (100% efficiency during winter, 78% during summer), we are unaware of any studies explicitly correlating air temperature (and thus indirectly correlating microbial activity) with scavenging efficiency by vertebrates. During summer months, Putman (1976) observed higher rates of scavenging in forested habitat (90%) than in grassland habitat (64%). He attributed this difference to a slower rate of decomposition in woodlands, apparently due to reduced levels of direct sunlight and thus lower temperatures, rather than a difference in scavenging pressure between habitats. Conversely, Simonetti *et al*. (1984) found little difference in scavenging efficiency between two shrubland patches varying in shrub cover from 45 to 90%. Obviously, much remains to be learned concerning the influences of environmental factors on scavenging activities.

In this study, we assessed the efficiency of forest scavengers on small mammal carcasses. We investigated the influence of carcass size, forest type, visual conspicuousness, and air temperature on the rate of carcass removal. We used remote photography to investigate the identity of specific species that scavenge, the

amount of elapsed time from carcass placement to carcass discovery, and the time of day when scavenging events occur. To our knowledge, this is the first study to photographically identify scavengers of small mammals.

Material and methods

Study site and selection of experimental points

This study was conducted at the 780-km^2 Savannah River Site (SRS), near Aiken, South Carolina, USA. The SRS is a nuclear facility owned and operated by the United States Department of Energy, and is designated as a National Environmental Research Park. Approximately 64% of the SRS is covered in loblolly pine *Pinus taeda*, longleaf pine *P. palustrus*, and slash pine *P. elliottii* (Workman and McLeod 1990), which is managed for timber by the United States Forest Service. An additional 15% of the land cover is classified as bottomland hardwood (Workman and McLeod 1990). For a more detailed description of the vegetation types of the SRS, see White and Gaines (2000) and Workman and McLeod (1990). The average annual rainfall at the SRS is 120 cm, and the average temperatures in winter and summer are 9°C 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) during the study period was selected for our research. Nine timber compartments and all "set-asides" (research areas that are permanently free from management activities), encompassing approximately 152 km^2, 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 from the habitat map were condensed into two distinct habitat classes representing the two forest types. The Animal Movements extension (Hooge and Eichenlaub 1997) in ArcView 3.2 was used to generate 48 geographically random point locations within each of the two habitat classes. The points, which served as experimental locations (UTM coordinates) for carcass placement, were uploaded to a Garmin 12CX handheld Global Positioning System (GPS) unit.

Field methods

Rodent carcasses were set out at each of the 96 random points during 6 consecutive 2-week periods (rounds), from 3 December 2000 through 3 March 2001. During each round, the influence of 3 dichotomous variables (habitat type, carcass size, and visual conspicuousness) on the number of carcasses removed by scavengers 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 divided into 2 sizes: mice *Mus musculus* averaged 19.4 g in mass (SD = 1.7, range 16–23) and rats *Rattus norvegicus* averaged 228 g (SD = 52, range 139–378). Both mice and rats were brown-furred and obtained frozen from a commercial rodent breeder (Perfect Pets, Inc.). The influence of visual conspicuousness of the carcasses on the number of carcasses removed by scavengers was examined by covering half of the carcasses with a thin layer of leaves or pine needles. During each of the 6 rounds, 1 carcass was placed at each of 16 points such that 2 points were assigned to each of the 8 possible combinations of the 3 dichotomous variables. Because points were used only once, we avoided the potential bias associated with animals learning the locations of carcasses.

For each round, all points were located and carcasses were set out on a single day. We approached points by car, and then traveled on foot to each point, which were at least 50 m from a road (usually a minor dirt or gravel road with little traffic). Points were located with the handheld GPS unit (10–30 m accuracy). Carcasses were handled with gloved hands and set out to thaw at room temperature for approximately 12 h prior to use. At each sampling point carcasses were dropped from a plastic bag directly onto the ground. If the carcass was assigned to the "covered" category of visual conspicuousness, a wooden pole was used to rake enough leaves or pine needles over the carcass so that it was completely covered.

Infrared-triggered game scouting cameras (Buckshot 35a, Foresite, Inc.) loaded with Kodak 800-speed film (12 exposures) were aimed at all experimental carcasses. The cameras were tested prior

to the study and reliably detected mammals and birds as small as eastern gray squirrels *Sciurus carolinensis* at 3 m. Time and date were automatically stamped on all photographs. Cameras were programmed to take 2 pictures (8 seconds apart) per trigger, and cameras were automatically deactivated for 1 minute between triggers. The cameras were attached to trees approximately 1.5 m from ground level and aimed down at the carcass at a 45° angle; thus cameras were approximately 2 m from the carcasses. The cameras were enclosed in a camouflaged cover, making them quite inconspicuous to humans. At the end of the 2-week rounds, film was collected and all cameras were removed from experimental points on a single day. If a carcass had been apparently removed from its location, a 2 m-radius circle centered at the bait location was searched thoroughly for carcass remains.

Camera sensitivity was heavily dependent on ambient air temperature. For example, at lower temperatures (5°C), large mammals (eg eastern coyote *Canis latrans*) triggered the cameras when standing approximately 0.5 m from the carcass. However, at higher temperatures (20°C) animals of similar size only activated cameras when touching or standing directly over the carcass. Additionally, some carcasses were visited by more than one species over the course of a round, and occasionally carcass locations were visited by vertebrates after baits were removed. Because half of the carcasses were covered, it was impossible in some instances to confidently identify the responsible scavenger from a series of visitors to a single carcass location. We were conservative when assigning a species to a scavenging event – we only did so when an animal was photographed removing a carcass or a single animal was photographed several times directly over a carcass. Otherwise, the species responsible for a scavenging event was recorded as "unknown".

Air temperature was recorded every 2 minutes at 2 m above ground with an automated weather station near the center of the SRS (Charles Hunter, Savannah River Technology Center, pers. comm.). Two-week average temperatures for a round were calculated from all of the 2-minute readings taken during that round.

Statistical analyses

We attempted to model the effects of forest type, carcass size, and visual conspicuousness on the probability of scavenging using multiple logistic regression (Hosmer and Lemeshow 1989). All 3 independent variables were manually entered into the regression equation as categorical covariates. The dichotomous dependent variable was carcass removal. The influence of average air temperature during a round on the number of carcasses removed during the round was examined using linear regression. Data from all experimental points ($n = 96$) were used for logistic and linear regression analyses of predictor variables on carcass removal. For descriptive analyses concerning time of day for scavenging events and elapsed time for carcass removal, only those scavenging events that had a particular species assigned to them were used. All statistical analyses were performed with SPSS 10.0 (Norusis 1999, SPSS 1999).

Results

Sixty-two of 96 carcasses (65%) were scavenged during the course of this study. Twenty-eight of 62 carcasses removed were in the upland pine class, whereas 34 were in the bottomland hardwood class. Thirty-two of the carcasses scavenged were mice and 30 were rats. Similarly, 32 were covered and 30 were uncovered. Logistic regression failed to produce any significant associations between the predictor variables and carcass removal.

For 36 of the 62 scavenged carcasses (58%), we were unable to determine the species responsible for removal. Eleven vertebrate species, 10 of which were mammals, scavenged the remaining 26 carcasses (Fig. 1A, Appendix). Raccoons *Procyon lotor* scavenged 7 carcasses, followed by gray foxes *Urocyon cinereoargenteus* (5 carcasses) and feral pigs *Sus scrofa* (3 carcasses). The mean (± SD) elapsed time (in days) for carcass removal was 5.6 ± 3.3 (Fig. 1B). Most carcasses were removed during the
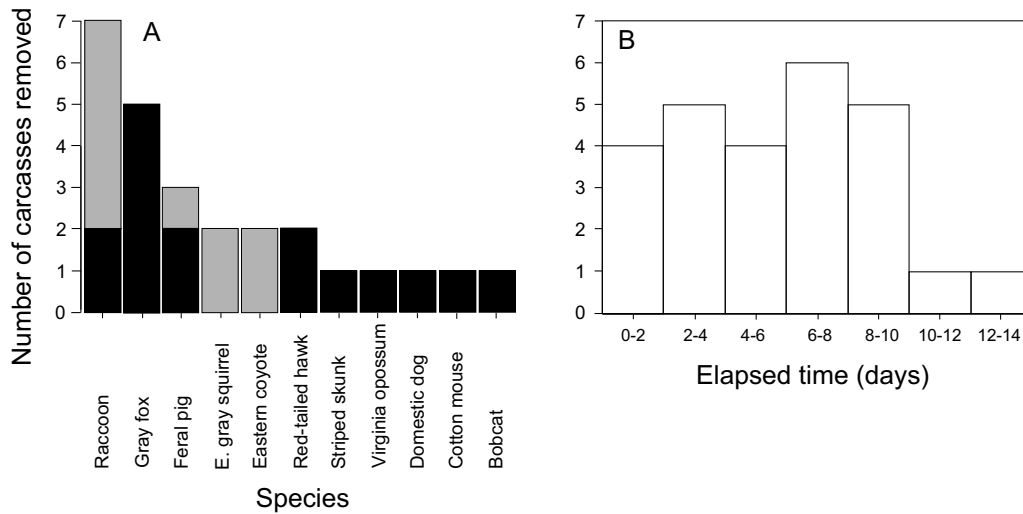
Fig. 1. Number of carcasses removed by vertebrates at the Savannah River Site, SC, during the winter of 2000–2001. Sixty-two of 96 (65%) carcasses were removed during the course of this study; 26 were assigned to a specific scavenger species (A). Dark bars represent rats, hatched bars represent mice. The mean elapsed time for carcass removal was 5.6 days (B). Latin names are as follows: bobcat *Lynx rufus*, cotton mouse *Peromyscus gossypinus*, domestic dog *Canis familiaris*, Virginia opossum *Didelphis virginiana*, striped skunk *Mephitis mephitis*, red-tailed hawk *Buteo jamaicensis*, eastern coyote *Canis latrans*, eastern gray squirrel *Sciurus carolinensis*, feral pig *Sus scrofa*, gray fox *Urocyon cinereoargenteus*, raccoon *Procyon lotor*.

night: 19 of 26 carcasses (73%) were removed between 18.00 and 08.00 hours. Many carcass locations were visited by a series of mammals, even after carcasses were scavenged. Although they were never the first species to a carcass location, nine-banded armadillos *Dasypus novemcinctus* were photographed at carcass locations on 4 occasions. Also, white-tailed deer *Odocoileus virginianus* were photographed on 5 occasions smelling carcasses or areas where carcasses had previously been located.

The influence of air temperature on the rate of carcass removal was striking (Fig. 2). Average temperature during rounds accounted for nearly all of the variance in the number of carcasses removed per round ($R^2 = 0.95$).
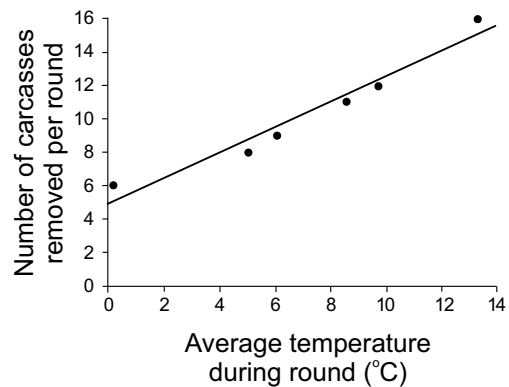

Fig. 2. Number of carcasses removed by scavengers per round in relation to average temperature (°C) during the round. The regression model was significant: $R^2 = 0.95$, $p = 0.001$, $y = 4.91 + 0.76x$.

Discussion

The percentage of carcasses removed during this study was lower than winter scavenging rates reported by Mullen and Pitelka (1972; 99%), Putman (1976; 100%), and Simonetti *et al*. (1984; 100%). However, studies investigating scavenging efficiency of bird carcasses report scavenging rates ranging from 13 to 100%, during various times of the year (Rosene and Lay 1963, Balcomb 1986, Tobin and Dolbeer 1990, Pain 1991). In addition, Putman (1976) did not reach 100% scavenging efficiency in winter until 33 days had elapsed, and Mullen and Pitelka (1972) placed carcasses under the snow in the Alaskan tundra "in the fall" and checked them the following springs, when they recovered less than 1% of the carcasses. Thus, limiting our experimental trials to 2 weeks may have caused us to underestimate carcass removal relative to other studies using longer trials. Camera malfunctions also may have affected our scavenging rate estimates. Since most scavenging events occurred during the night, a flash was required for the photographs. Frequently, cameras failed to flash on the first picture when they were triggered. When this happened, the second picture (8 seconds after the initial picture) always flashed, but often showed no animal in the scene. It was likely that on occasion, noise from the first photograph (without a flash) frightened potential scavengers away from carcasses before the second photograph was taken. Efforts are currently underway to develop a more reliable camera system.

There is experimental evidence that carcasses decompose more rapidly at elevated temperatures, primarily due to increased activity by arthropods, bacteria, and fungi, and thus emit odors more rapidly (Putman 1978, Shean *et al*. 1993). However, existing research indicates that scavenging pressure is roughly equivalent during summer and winter periods, suggesting that visual cues may play a larger role in carcass discovery than do olfactory (Putman 1976, 1983). Interestingly, the strong positive relationship we observed between ambient air temperature and carcass removal in combination with our finding of equal rates of scavenging on covered and uncovered carcasses provides compelling evidence that olfactory rather than visual cues were the overriding signals attracting scavengers, primarily mammals, to carcasses. The presence of mammals at carcass locations after removal also suggests that scent was integral to carcass discovery. Furthermore, research by Shivik and Clark (1997) and Shivik (1999) indicated that like mammals, brown treesnakes *Boiga irregularis* also primarily use chemical cues to locate carrion.

If indeed olfactory cues are the overriding signals advertising edible carcasses, it creates an interesting evolutionary problem. Janzen (1977) hypothesized that odors emitted from decomposing carcasses have evolved as honest signals given off by microbes that advertise their toxicity to larger organisms. In this way, Janzen suggested, microbes can compete with vertebrates for carrion resources. However, data from the present study indicate that carrion odors actually attract vertebrates to carcasses. Another possibility, alluded to by Janzen (1977), and more consistent with the data presented here, is that odors attract insects and vertebrates to

carcasses for the purpose of opening and burrowing through them, thereby creating previously inaccessible habitat for microbes to occupy. Carrion insects have been shown to facilitate decomposition by microbes: even at summer temperatures, carrion tends to mummify rather than decompose when insects are excluded (Payne 1965, Janzen 1977). Future work directly concerned with elucidating the cues used by vertebrates to locate carcasses, as well as the competition between microbes and vertebrates for this resource, would be highly beneficial.

Scavenging provides an important source of nourishment for many facultative scavengers, especially during winter months when competition with microbes is limited. The data presented in this paper, combined with previous studies (eg Putman 1976), indicate that small carcasses, when available, are readily used by a variety of mammalian carnivores. However, the extent to which vertebrates use carrion remains unclear, and undoubtedly varies among species. We feel that current views on food habits of some facultative scavengers should be reevaluated, with more emphasis on attempting to discern prey items from scavenged items.

References

Balcomb R. 1986. Songbird carcasses disappear rapidly from agricultural fields. Auk 103: 817–820.

Bobek B. 1969. Survival, turnover and production of small rodents in a beech forest. Acta Theriologica 14: 191–210.

Bobek B. 1973. Net production of small rodents in a deciduous forest. Acta Theriologica 18: 403–434.

Cooper S. M., Holekamp K. E. and Smale L. 1999. A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). African Journal of Ecology 37: 149–160.

Cowles R. B. and Phelan R. L. 1958. Olfaction in rattlesnakes. Copeia 1958: 77–83.

Halley D. J. and Gjershaug J. O. 1998. Inter- and intra-specific dominance relationships and feeding behaviour of Golden Eagles *Aquila chrysaetos* and Sea Eagles *Haliaeetus albicilla* at carcasses. Ibis 140: 295–301.

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. Ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska.

Hosmer D. W. and Lemeshow S. 1989. Applied logistic regression. Wiley and Sons, New York: 1–307.

Houston D. C. 1979. The adaptations of scavengers. [In: Serengeti, dynamics of an ecosystem. A. R. E. Sinclair and M. N. Griffiths, eds]. University of Chicago Press, Chicago: 263–286.

Janzen D. H. 1977. Why fruits rot, seeds mold, and meat spoils. The American Naturalist 111: 691–713.

Jones M. E. 1998. The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. Animal Behaviour 56: 1279–1284.

McKillup S. C. and McKillup R. V. 1994. The decision to feed by a scavenger in relation to the risks of predation and starvation. Oecologia 97: 41–48.

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: 1–82.

Pain D. J. 1991. Why are lead-poisoned waterfowl rarely seen?: the disappearance of waterfowl carcasses in the Camargue, France. Wildfowl 42: 118–122.

Payne J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46: 592–602.

Putman R. J. 1976. Energetics of the decomposition of animal carrion. PhD thesis, University of Oxford, Oxford: 1–131.

Putman R. J. 1978. Patterns of carbon dioxide evolution from decaying carrion. Decomposition of small mammal carrion in temperate systems 1. Oikos 31: 47–57.

Putman R. J. 1983. Carrion and dung: the decomposition of animal wastes. Edward Arnold, London: 1–62.

Rosene W. and Lay D. W. 1963. Disappearance and visibility of quail remains. The Journal of Wildlife Management 27: 139–142.

Shean B. S., Messinger L. and Papworth M. 1993. Observations of differential decomposition on sun exposed v. shaded pig carrion in coastal Washington State. Journal of Forensic Sciences 38: 938–949.

Shivik J. A. 1999. Carrion, context, and lure development: the relative importance of sensory modalities to foraging brown treesnakes (*Bioga irregularis*). PhD thesis, Colorado State University, Fort Collins: 1–121.

Shivik J. A. and Clark L. 1997. Carrion seeking in brown tree snakes: importance of olfactory and visual cues. Journal of Experimental Zoology 279: 549–553.

Simonetti J. A., Yanez J. L. and Fuentes E. R. 1984. Efficiency of rodent scavengers in central Chile. Mammalia 48: 608–609.

SPSS. 1999. SPSS base 10.0 applications guide. SPSS, Inc., Chicago: 1–426.

Tobin M. E. and Dolbeer R. A. 1990. Disappearance and recoverability of songbird carcasses in fruit orchards. Journal of Field Ornithology 61: 237–242.

Wallace M. P. and Temple S. A. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104: 290–295.

White D. L. and Gaines K. F. 2000. The Savannah River Site: site description, land use, and management history. Studies in Avian Biology 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, South Carolina.

Wilton M. L. 1986. Scavenging and its possible effects upon predation – a selective review of literature. Alces 22: 155–180.

Workman S. K. and McLeod K. W. 1990. Vegetation of the Savannah River Site: major community types. SRO-NERP-19. Savannah River Ecology Laboratory, South Carolina: 1–137.

Appendix. Number of scavenging events assigned to specific species for each combination of predictor variables. Codes are as follows: u – upland pine, b – bottomland hardwood, m – mouse, r – rat, c – covered, n – uncovered. Studies were conducted at the Savannah River Site, SC, during the winter of 2000–2001.

Variables	Raccoon	Gray fox	Feral pig	Eastern coyote	E. gray squirrel	Red-tailed hawk	Bobcat	Cotton mouse	Dog	Virginia opossum	Striped skunk	Unknown	Total
u-m-c				1								6	7
u-m-n	2											4	6
u-r-c		2										6	8
u-r-n		2										5	7
b-m-c	1											8	9
b-m-n	2		1	1	2							4	10
b-r-c	1	1	1			1		1	1	1	1		8
b-r-n	1		1			1	1					3	7
Total	7	5	3	2	2	2	1	1	1	1	1	36	62