
FORAGING ECOLOGY OF THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*) IN A FRAGMENTED AGRICULTURAL LANDSCAPE

ROD D. WITTENBERG

Department of Biological Sciences, The University of Arkansas, 601 Science Engineering, Fayetteville, Arkansas 72701, USA
Current affiliation: U.S. Fish and Wildlife Service, Ruby Lake National Wildlife Refuge,
Ruby Valley, Nevada 89833, USA, e-mail: rod_wittenberg@fws.gov

Abstract.—Habitat loss and fragmentation pose perhaps the greatest threats to snake populations, yet information is sparse. Despite habitat fragmentation being cited as a primary threat to the Timber Rattlesnake (*Crotalus horridus*), our knowledge of the foraging ecology of this species is largely based on studies conducted in mature forests. Here, I present data obtained from a 4-y study of Timber Rattlesnakes in west-central Missouri where snakes readily foraged in secondary woodland tracts and corridors, agricultural fields, and habitat edges. Dietary analysis found that snakes fed exclusively on mammals, including shrews (Soricidae), mice in the genus *Peromyscus*, Prairie Voles (*Microtus ochrogaster*), Cotton Rats (*Sigmodon hispidus*), Eastern Gray Squirrels (*Sciurus carolinensis*), and Eastern Cottontails (*Sylvilagus floridanus*). Although small mammal trapping indicated that fields contained fewer numbers of prey than woodlands and habitat edges, field dwelling Prairie Voles were the most frequently consumed prey item. Arboreal foraging and ambush strategies utilizing logs and tree trunks were not prevalent in the study population. Although anthropogenic mortality among snakes using fields suggests fields may function as ecological traps, the present study indicates that large tracts of mature forest are not required for Timber Rattlesnakes to forage effectively. Therefore, prey availability may be more important to this species than the structural habitat in which it forages.

Key Words.—*Crotalus horridus*; diet; foraging ecology; habitat fragmentation; Timber Rattlesnake

INTRODUCTION

Studies of terrestrial vertebrates in fragmented habitats have primarily focused on birds and mammals, while in these same habitats, reptiles and amphibians remain largely unstudied (Mac Nally and Brown 2001; Heard et al. 2004). Conservation efforts targeting reptiles and amphibians have been significantly undermined because little is known regarding their natural history in human-impacted landscapes (Bury 2006). To successfully manage herpetofauna, researchers cannot strictly rely on past studies conducted in pristine habitats (Bury 2006). According to Dodd (1987), the greatest threat posed to snakes is habitat destruction. In North America, loss of snake habitat has occurred primarily from residential and agricultural development, logging and forestry practices, and the impoundment of streams and rivers (Dodd 1987).

The Timber Rattlesnake (*Crotalus horridus*) is a North American snake species threatened by loss and fragmentation of closed-canopy forests (Martin 1992; Brown 1993; Clark et al. 2003; Furman 2007). This well-studied pitviper inhabits forested regions of central and eastern North America (Brown 1993) where it is considered to be an important forest-floor predator (Reinert et al. 2011a) that favors mature woodlands with a high degree of canopy closure (Collins and Knight 1980; Reinert 1984; Reinert and Zappalorti 1988; Martin 1992; Rudolph et al. 1998). In fact, most ecological

studies of Timber Rattlesnakes have been conducted in mature forests lacking large-scale habitat heterogeneity (reviewed in Wittenberg 2009). Thus, despite the threat posed by habitat fragmentation to the Timber Rattlesnake, our understanding of the foraging ecology of this species is based primarily from research on forest dwelling populations (Reinert et al. 1984; Brown and Greenberg 1992; Clark 2006a,b; Reinert et al. 2011a). Efforts to conserve declining Timber Rattlesnake populations in fragmented forests may be enhanced by studying how individuals acquire prey in more open, disturbed habitats.

From April 2003 through May 2007, I studied the foraging ecology of a Timber Rattlesnake population in west-central Missouri that inhabited a fragmented, agricultural landscape. I used data obtained through dietary analysis, radio telemetry, and small mammal trapping to answer three primary questions regarding the foraging ecology of snakes in this population. 1) What are the types of habitat (i.e., woodland, field, or edge) where individuals forage? 2) What types of prey species are being consumed? and 3) How do relative prey abundances vary among the different foraging habitats? Finally, I discuss how the foraging behavior and diet of the study population compares to that of previously studied populations of Timber Rattlesnakes in closed-canopy forests.



FIGURE 1. Representative portion of the study site of foraging ecology of Timber Rattlesnakes (*Crotalus horridus*) showing landscape fragmented by agriculture. Individual dots represent one or more radio telemetry relocations of a 100.0 cm SVL male Timber Rattlesnake (# 150) that was relocated 43 times between 3 October 2004 and 28 August 2006. In 2005 and 2006, male 150 emerged from the same hibernaculum and traveled northeast to forage in habitat edges, fields, and wooded creek-bottoms. The maximum distance relocated from the hibernaculum was 1.7 km. Lines represent estimates of home range and core areas (detailed in Wittenberg 2009). Aerial image obtained from Missouri Spatial Data Information Service.

MATERIALS AND METHODS

Study site.—The study area is a highland region of west-central Missouri considered part of the prairie geographic region (Schwartz and Schwartz 1959). The highlands consist of hills with hardwood forests that extend across a flat landscape of what was once tall grass prairie (Schwartz and Schwartz 1959; Sims 1988). This historical intermingling of closed and open canopy habitats has been further diversified by human land use practices. Anthropogenic habitat fragmentation has created a geometric patchwork of small woodlots, narrow wooded fencerows, agricultural fields, residences, and roads (Fig. 1). An approximately 32 ha inactive rock quarry provides hibernacula for all Timber Rattlesnakes in the study population. Remnant boulder piles located throughout the quarry are used as rookery habitat for gestating females during summer months. Males and non-pregnant females spend much of the summer foraging in three major habitat types that can be broadly defined by degree of canopy closure. The three habitat types are woodland (mostly small tracts and corridors of secondary woodlands), field (old fields in various stages of succession, grassy hay fields, and row crops of soybean and corn), and edge (primarily areas where woodlands and fields converge).

Study animals.—I surgically implanted radio transmitters (Holohil Systems models SI-2, SI-2T, and SB-2T, Carp, Ontario, Canada) into the coelomic cavities of 26 Timber Rattlesnakes (13 males, 13 females) following the protocol of Reinert and Cundall (1982). I measured snout-vent lengths (SVL) of implanted snakes in a squeeze box (Quinn and Jones 1974) and SVLs ranged from 68.0 to 101.2 cm. Body masses ranged from 245 to 1126.5 g prior to implantation and transmitter mass (range 5.2–14.2 g) never exceeded 5% of the total body mass of a snake. During the study, 10 of the 13 females were pregnant for one season.

Observations of foraging behavior.—Telemetry relocations provided the basis for observational data on the foraging habits of snakes in the study population. Initial study design called for snakes to be tracked every 3–4 d, although this was not always possible. I pooled telemetry relocations of non-hibernating snakes across field seasons and the monthly distribution of these relocations reflected seasonal patterns of egress and ingress (March = 0.4%, April = 5.7%, May = 9.9%, June = 15.3%, July = 28.3%, August 21.2%, September 14.7%, October 4.6%). I determined snakes to be foraging when I observed them in a typical ambush



FIGURE 2. Male Timber Rattlesnake (*Crotalus horridus*; 88.2 cm SVL) coiled in ambush at the interface of a woodland corridor and a soybean field. (Photographed by Rod D. Wittenberg).



FIGURE 3. Location of Timber Rattlesnake (*Crotalus horridus*) depicted in Figure 2. The snake was foraging in lush undergrowth directly behind the white bucket. Ground cover often impeded behavioral observations in edges and fields. (Photographed by Rod D. Wittenberg).

posture (Beaupre 2008; Reinert et al. 2011a), and in nearly all cases, I found ambushing individuals on the surface in a tight, concentric coil. The neck extended from the middle of this coil in an S-shaped fashion, allowing the head to rest upon an outer coil of the body (Fig. 2). From this position, individuals can readily strike passing prey (Cundall and Beaupre 2001). I did not consider snakes to be foraging if they were in ecdysis, digesting prey (which could only be determined if the body was visibly distended), moving, associating with another individual of the opposite sex, or gestating. Lush undergrowth associated with edge habitats (Fig. 3) and the dense tussocks of vegetation in fields made observing snakes in these habitats difficult. Often, I could only see all or part of an individual by slightly moving the concealing vegetation. I did not manipulate vegetation if disturbing the snake was likely, thus preventing snakes from being directly observed in 16.9% of edge and 22.4% of field relocations. By contrast, snakes were at least partially visible during 95.6% of woodland relocations. Because snake behavior could not be determined if the individual was concealed by surface vegetation, I likely underestimated instances of foraging in edges and fields.

Diet analysis.—I collected 30 fecal samples opportunistically from snakes while they were held in captivity for mark-recapture processing or radio transmitter implantation/removal. I recorded the identities of individual snakes that deposited feces so that dietary data could be analyzed with respect to snake size and sex. Snakes were occasionally transported or housed together which did not allow feces to be assigned

to an individual. Five of 12 Timber Rattlesnakes killed while crossing roads at the study site contained dietary material. I explored the entire digestive tract of each road-killed specimen to recover prey items from the stomach as well as hindgut contents distributed throughout the intestines. Finally, I recovered dietary material from the scattered remains of two telemetry subjects killed by farm implements, bringing the total number of dietary samples examined to 37.

I dissected feces and hindgut contents recovered from salvaged specimens in a Petri dish containing 70% ethanol. I used a dissecting microscope to identify consumed prey items to vertebrate class owing largely to the presence of undigested hair. I cleaned and mounted samples of the hair on microscope slides for further examination using a compound light microscope. Characteristics such as hair length, width, color, shape, cuticular scale pattern, cortex width, and medullary configuration can be used to identify mammals to the species level (Mayer 1952; Tumilson 1983). Using Burt and Grossenheider (1980) and Schwartz and Schwartz (1959), I compiled a comprehensive list of mammals that as juveniles or adults might serve as prey for Timber Rattlesnakes and have ranges that overlapped or approached my study site. Guided by this list, I constructed a reference set of microscope slides using mammal skins from the University of Arkansas Museum Collections. I identified prey by comparing slides of hair recovered from feces to the reference slides of hair obtained from mammals of known identity. Additionally, 51% of dietary samples (including feces) contained undigested mammal skeletal fragments and/or

teeth. Cranial components and teeth greatly facilitated identification of dietary samples.

Mammal trapping.—To determine if relative prey abundance could explain the use of disturbed habitat by Timber Rattlesnakes, I trapped small mammals in woodland, field, and edge habitats during periods of the active season when snakes were typically foraging. During July and August of 2005, I conducted four trapping sessions to compare relative mammal abundances in woodland habitats to those in fields and edges. Trapping sessions one and three directly compared woodland tracts to uncut grassy fields. Trapping sessions two and four directly compared woodland tracts to wooded fencerows (edge habitat). A trapping session consisted of simultaneously placing 60 traps in each of the two habitats for three nights. I conducted two additional trapping sessions in June of 2006, in which 40 traps were placed in all three habitats simultaneously. To better understand small mammal diversity at the study site, I never conducted trapping sessions in the same specific location more than once throughout the study. Therefore, six woodland tracts, four uncut grassy fields, and four wooded fencerows were sampled during the six trapping sessions.

Trapping grid configuration was rectangular, and although the shape of the rectangle varied to accommodate the habitat, the distance between adjacent traps was always 10 m. For instance, because wooded fencerows were approximately 10 m wide, I placed traps in two parallel rows along opposing edges of this habitat. Consequently, grid configurations in edge habitat were long and narrow compared to those in woodland tracts and fields. I opened non-folding Sherman live traps in the evening just before sunset and closed each trap in the morning after it was checked. Closing traps during the day prevented trapping mammals when they could be subjected to lethal temperatures. I baited traps with a mixture of oats and peanut butter. I identified captured mammals to species, weighed, and gave them a batch-mark before they were released.

The activity patterns of small mammals can vary on a temporal scale and are affected by weather and moonlight (Stokes et al. 2001). Therefore, because all three habitats were not trapped simultaneously during trapping sessions one through four, I did not pool capture data across all six trapping sessions by habitat type. Instead, I first compared habitat-specific capture data independently within each of the six trapping sessions. I recorded 232 capture events during the study, 85 (36.6%) of which were recaptures of individuals captured and marked during the first or second night of a given trapping session. I only reported data pertaining to first-captures and analyzed these data herein. Contingency table analyses ($\alpha = 0.05$) tested the null hypothesis that the number of small mammals captured

in fields and edges would not differ from those captured in woodlands. Because I only trapped two habitats simultaneously during 2005 (trapping sessions 1–4), I analyzed capture data using 2×2 contingency tables and the Fisher exact test (Zar 1999). I trapped three habitats simultaneously in 2006 (trapping sessions 5 and 6) and therefore I analyzed capture data using 3×2 contingency tables and the Chi-square test (Zar 1999). I performed contingency table analyses using JMP version 8.0.1 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Observations of foraging behavior.—I made 627 telemetry observations of Timber Rattlesnakes in habitats classified as either woodland ($n = 69$), field ($n = 80$), edge ($n = 66$), quarry ($n = 398$), or other ($n = 14$). Within the quarry, I often relocated snakes in boulder piles (transient habitat and birthing rookeries), rocky slopes and outcroppings (hibernacula), and to a lesser degree, anthropogenic material that included scrap metal and discarded tires. I could not assign the small number of relocations classified as “other” to the other four habitat types (i.e., snakes near roads). In woodland, field, edge, quarry, and other habitats, I observed foraging in 53.6, 47.5, 66.7, 1.0, and 7.1% of relocations, respectively. Although individuals were given sufficient time to move into a different habitat between relocations (typically days), these data represent repeated observations of 26 individual radio telemetry subjects. Snakes did exhibit individual tendencies with respect to where they foraged. Nevertheless, of the 15 individuals I observed foraging more than once, 13 foraged in more than one habitat type (Table 1). Despite a repeated-measures bias, the telemetry data clearly showed that snakes in the study population foraged in woodland, field, and edge habitat.

Diet analysis.—I identified 41 mammalian prey items from 37 dietary samples (Fig. 4). Prairie Voles (*Microtus ochrogaster*) comprised 41.5% of the identified prey. The remaining prey consisted of 24.4% *Peromyscus* mice, 14.6% Cotton Rats (*Sigmodon hispidus*), 9.8% shrews (Soricidae), 4.9% Eastern Cottontail Rabbits (*Sylvilagus floridanus*), 2.4% Eastern Gray Squirrels (*Sciurus carolinensis*), and 2.4% unidentified mammal (owing to a small and degraded hair sample). Larger prey such as rats, rabbits, and squirrels were only consumed by large individuals. However, smaller prey such as shrews, mice, and voles were not excluded from the diet of larger individuals (Fig. 5). Sexual differences in types of prey consumed were not apparent. Although I only recovered shrews from females, this is most likely an artifact of small sample size ($n = 4$).

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TABLE 1. Records of habitat use and foraging behavior within each habitat for 26 radio-tagged Timber Rattlesnakes (*Crotalus horridus*; 13 males, 13 females). Values represent the number of telemetry relocations occurring in each habitat type, values in parentheses represent the number of telemetry relocations where foraging was observed. "Other" relocations describe those occurring in habitats that could not be characterized as woodland, field, edge, or quarry.

Snake ID	Sex	Woodland relocations	Field relocations	Edge relocations	Quarry relocations	Other relocations	Total relocations
150	male	16 (11)	7 (5)	10 (8)	17 (0)	0	50
260B	male	3 (1)	5 (3)	6 (3)	21 (0)	0	35
215	male	9 (7)	7 (2)	3 (3)	0	3 (0)	22
760A	male	0	0	0	8 (1)	1 (0)	9
240	male	1 (1)	6 (2)	2 (1)	10 (0)	0	19
210	male	3 (0)	7 (3)	4 (4)	18 (0)	1 (0)	33
802	male	5 (2)	0	9 (6)	11 (0)	1 (0)	26
709	male	0	3 (1)	0	14 (0)	0	17
099	male	3 (2)	8 (2)	8 (7)	11 (0)	1 (0)	31
193	male	15 (4)	0	6 (3)	15 (0)	0	36
170A	male	3 (0)	1 (0)	1 (0)	0	0	5
170B	male	0	0	0	6 (0)	0	6
032	male	0	0	1 (1)	0	1 (0)	2
275	female	8 (7)	10 (8)	1 (0)	8 (0)	0	27
260A	female	0	4 (3)	0	0	0	4
760B	female	0	1 (1)	4 (3)	25 (0)	0	30
340	female	1 (1)	1 (1)	3 (1)	15 (0)	0	20
528	female	0	0	0	33 (1)	0	33
909	female	0	1 (1)	0	28 (1)	2 (1)	31
731A	female	0	2 (1)	0	30 (0)	0	32
731B	female	0	0	0	10 (0)	0	10
821	female	0	14 (4)	0	25 (0)	4 (0)	43
669	female	0	0	0	29 (0)	0	29
120	female	0	1 (0)	1 (0)	19 (0)	0	21
411	female	2 (1)	0	0	18 (0)	0	20
060	female	0	2 (1)	7 (4)	27 (1)	0	36
Total	—	69 (37)	80 (38)	66 (44)	398 (4)	14 (1)	627

Four samples contained two prey items. A single road-killed specimen contained a relatively intact Prairie Vole in its stomach and Cotton Rat hair in its large intestine. Three other snakes had each consumed two Prairie Voles, as was evident by the presence of two distinct skulls. Other items I recovered from feces and hindgut included straw-like vegetation, exoskeletons of small insects, and shed fangs. The vegetation was likely inadvertently swallowed during ingestion. Secondary consumption would explain the presence of insect exoskeletons, as these were recovered with *Peromyscus* hair. Mice in the genus *Peromyscus* are known to occasionally eat insects (Burt and Grossenheider 1980). No fewer than nine dietary samples contained shed fangs (24.3%), and as many as six fangs were recovered from a single sample.

Mammal trapping.—In 2005, two trapping sessions (1 and 3) compared small mammal captures in woodlands to those in fields (Table 2). Woodland habitat produced significantly more captures than field habitat during session three but not during session one (Table 2). Similarly, two trapping sessions (2 and 4) comparing captures in woodland and edge habitats were also split with respect to their statistical significance

(Table 2). Edge habitat produced significantly more captures than woodland habitat during session four but not during session two.

In 2006, two trapping sessions (5 and 6) compared woodland, field, and edge habitats simultaneously (Table 2). Significant differences in captures among the three habitats were detected in both sessions five and six (Table 2). During both sessions the number of captures in woodland and edge habitats was similar; however, woodlands produced markedly more captures than fields.

The contingency table analyses indicate that woodland and edge habitats did not differ in three of the four sessions where both habitats were trapped simultaneously (Table 2). In contrast, woodlands produced more captures in three of the four sessions where both woodland and field habitats were trapped simultaneously (Table 2). On the basis of trapping effort, edge habitat was the most productive (75 captures, 600 trap nights, capture rate = 12.5 captures per 100 trap nights), followed by woodlands (57 captures, 960 trap nights, capture rate = 5.94 captures per 100 trap nights) and fields (15 captures, 600 trap nights, capture rate = 2.5 captures per 100 trap nights; Table 3). However, habitat-specific capture rates obtained by pooling data across trapping sessions (i.e.,

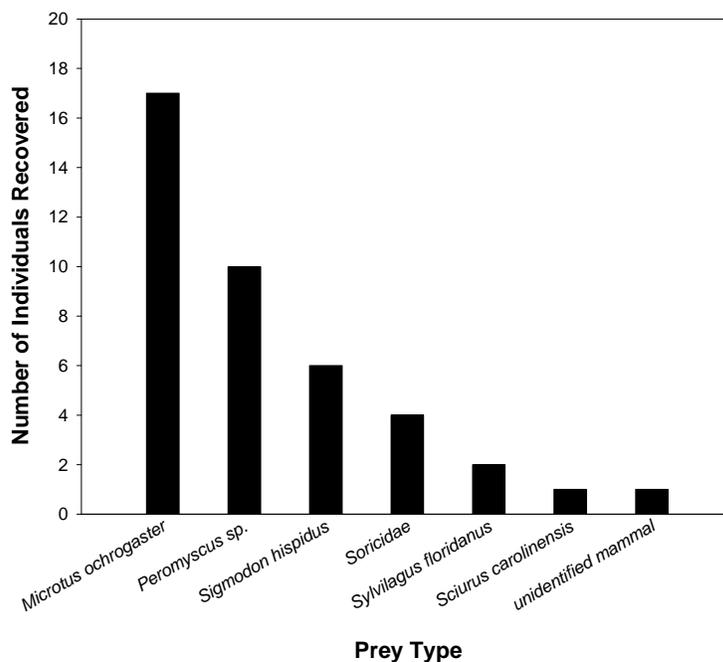


FIGURE 4. Total number of each type of mammal prey recovered from Timber Rattlesnakes (*Crotalus horridus*) in the study population. Identified prey included shrews (Soricidae), mice in the genus *Peromyscus*, Prairie Voles (*Microtus ochrogaster*), Cotton Rats (*Sigmodon hispidus*), an Eastern Gray Squirrel (*Sciurus carolinensis*), and Eastern Cottontails (*Sylvilagus floridanus*).

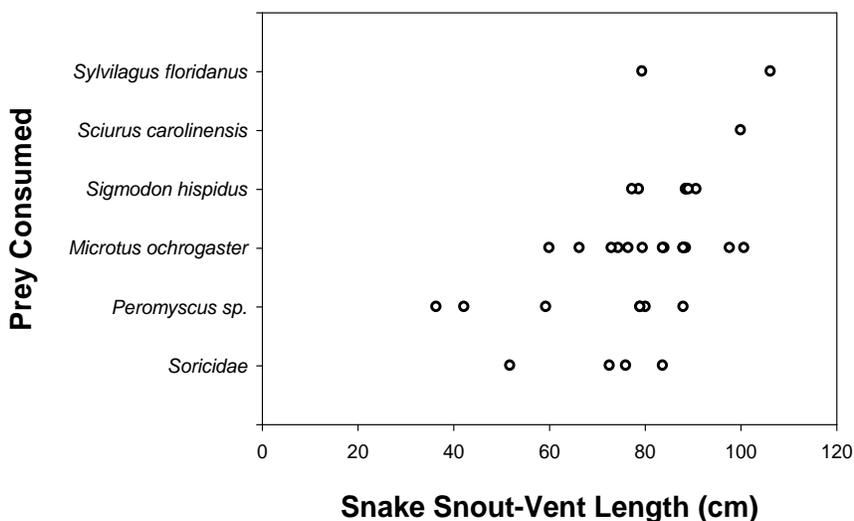


FIGURE 5. Relationship between snake size (snout-vent length) and type of mammal prey consumed, based on 33 dietary samples collected from individuals of known identity. Prey are ordered on the Y-axis by ascending average adult body mass.

time periods) should be interpreted cautiously, given that field and edge habitats were not trapped simultaneously in sessions 1 through 4.

Mice in the genus *Peromyscus* (*P. leucopus* and *P. maniculatus*) accounted for the majority of both

woodland (96.5%) and edge (61.3%) captures (Table 3). Cotton Rats were also prevalent in habitat edges (32.0%; Table 3). Despite a paucity of captures, fields produced the greatest diversity of species (n = 6; Table 3). Prairie Voles were the most frequently captured mammal in

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TABLE 2. Results of contingency table analyses testing the null hypothesis that the number of small mammals captured in fields and edges would not differ significantly from those captured in woodlands. Because only two habitats were trapped simultaneously during 2005 (trapping sessions 1–4), capture data were analyzed using 2×2 contingency tables and the Fisher exact test. Three habitats were trapped simultaneously during 2006 (trapping sessions 5, 6) and capture data were therefore analyzed using 3×2 contingency tables and the Chi-square test.

Trapping session	Three-day trapping period	Traps per habitat	Habitat type	Captures	Non-captures	Test	P-value
2005 Trapping							
1	15-18 July, 2005	60	Woodland Field	11 9	169 171	Fisher exact	0.819
2	26-29 July, 2005	60	Woodland Edge	8 11	172 169	Fisher exact	0.639
3	06-09 August, 2005	60	Woodland Field	10 2	170 178	Fisher exact	0.036*
4	12-15 August, 2005	60	Woodland Edge	0 32	180 148	Fisher exact	< 0.001*
2006 Trapping							
5	14-17 June, 2006	40	Woodland Field Edge	18 3 15	102 117 105	Chi-square = 11.667	0.003*
6	24-27 June, 2006	40	Woodland Field Edge	10 1 17	110 119 103	Chi-square = 14.948	< 0.001*

fields (40.0%), the only habitat in which they were detected (Table 3).

DISCUSSION

Observations of foraging behavior.—Studies conducted in mature woodlands suggest that logs and trees are important to foraging Timber Rattlesnakes. In Pennsylvania, Reinert et al. (1984) described coiled Timber Rattlesnakes placing their chins on the lateral surface of logs to ambush mammals using the log as a

runway. The authors indicated that this was the “typical” ambush posture of individuals in the population and suggested that “fallen logs play a functional role in the predatory behavior of this species.” More recently, the prevalence of this log-oriented ambush behavior has been observed to vary among populations in the forests of Pennsylvania and New Jersey (Reinert et al. 2011a). In northeastern New York, Brown and Greenberg (1992) documented an adult male Timber Rattlesnake adopting an upward-facing ambush posture at the base of trees. The same vertical-tree

TABLE 3. Number of individual small mammal species captured in woodland, field, and edge habitats. Values in parentheses represent the percentage contribution made by that species to the total number of first-captures recorded in that habitat type. The number of trap nights in each habitat represent trapping effort, and were calculated by multiplying the number of traps deployed by the number of nights trapped. Captures per 100 trap nights were calculated by dividing the number of first-captures by the number of trap nights and multiplying the quotient by 100. Species are *Blarina brevicauda* (Bb), *Microtus ochrogaster* (Mo), *Mus musculus* (Mm), *Peromyscus leucopus* (Pl), *Peromyscus maniculatus* (Pm), *Reithrodontomys megalotis* (Rm), and *Sigmodon hispidus* (Sh).

Habitat	Bb	Mo	Mm	Pl	Pm	Rm	Sh	Trap nights	Total captures	Captures per 100 trap nights
Woodland	—	—	—	52 (91.2)	3 (5.3)	1 (1.8)	1 (1.8)	960	57	5.94
Field	—	6 (40.0)	1 (6.7)	1 (6.7)	3 (20.0)	1 (6.7)	3 (20.0)	600	15	2.50
Edge	1 (1.3)	—	4 (5.3)	42 (56.0)	4 (5.3)	—	24 (32.0)	600	75	12.50

ambush posture has been observed in south-central Indiana, where adult Timber Rattlesnakes select microhabitats based on the presence of tree trunks and log cover (Walker 2000). In South Carolina, 31% of foraging by female Timber Rattlesnakes occurred near logs, while 23% of foraging by males occurred at the base of trees (Waldron et al. 2006).

The ambush posture described by Reinert et al. (1984) was not prevalent among snakes in this study. On a single occasion, I observed a large adult male adopt this posture on a man-made pile of woody debris. Secondary woodlands and wooded fencerows typically lacked sizeable deadfall, which may provide a simple explanation as to why individuals did not display log-oriented ambush behavior. Although mature forest containing significant deadfall was present at the study site, few telemetry relocations occurred in this habitat. Interestingly, this mature forest was the only woodland habitat that failed to produce a single capture when trapped for small mammals (trial 4, Table 2). Furthermore, snakes were never observed foraging at the base of trees as described by Brown and Greenberg (1992).

The tendency for Timber Rattlesnakes to climb trees is well documented (Klauber 1972; Saenz et al. 1996; Coupe 2001; Sealy 2002; Rudolph et al. 2004). Rudolph et al. (2004) suggest foraging may provide the most general explanation for arboreal behavior (but see Fogell et al. 2002b; Bartz and Sajdak 2004). While both arboreal mammals and birds are consumed by Timber Rattlesnakes, the only natural observation of arboreal predation involved the striking and holding of avian prey (Sajdak and Bartz 2004). On a single occasion, I observed an adult female (77.4 cm SVL, 364 g) lying elongate approximately 2 m above the ground in an understory tree but I could not discern if she was foraging.

In the forests of New York, Clark (2006a) found that 81% of Timber Rattlesnake feeding events occurred at night and estimated that snakes fed successfully 12 to 15 times per year. In this study, snakes were never observed consuming prey but were found with visibly distended midbodies on five different occasions, indicating they had recently ingested prey. Because most radio telemetry relocations occurred during the day, the lack of feeding observations support those of Clark (2006a) that prey capture typically occurs at night. If his estimates of feeding frequency are accurate, it seems that individuals with visible body distensions should have been encountered more often. However, small prey may not be visually detected when consumed by relatively large snakes (Nowak et al. 2008; Repp and Schuett 2008). Furthermore, concealing surface vegetation often made diagnosing snake behavior difficult.

Keenlyne (1972) found that during the period of time between ovulation and parturition, pregnant female Timber Rattlesnakes in Wisconsin remained near large rocks and probably did not feed. Similarly, pregnant females in this study gestated exclusively within the rock quarry while other members of the population dispersed to forage in surrounding habitats. During 123 relocations of gestating females ($n = 10$), predatory behavior was never definitively observed. Pregnant females remained beneath rocks or within boulder piles much of the time. Although pregnant females were occasionally found tightly coiled on the surface near their chosen “maternal rock,” it did not appear that they were ambushing prey.

At least some females in the study population forage during seasons in which they reproduce, prior to gestation and/or following parturition (Wittenberg 2009). Successful spring foraging prior to gestation, coupled with a long fecal retention time characteristic of vipers (Lillywhite et al. 2002), might explain why I collected feces containing hair from seven pregnant females. Although Keenlyne (1972) dissected 23 reproductive females and reported finding no prey items, it is unclear if the author examined the lower digestive tract for feces or hindgut contents.

Diet analysis.—Recovering only mammalian prey in the feces and digestive tracts of Timber Rattlesnakes from west-central Missouri is consistent with other dietary studies of this species. Regional studies in Arkansas (Montgomery 2005), Georgia (Hamilton and Pollack 1955; Parmley and Parmley 2001), New Jersey (Reinert et al. 2011a), Pennsylvania (Surface 1906; Reinert et al. 1984; Reinert et al. 2011a), Tennessee (Savage 1967), Virginia (Uhler et al. 1939; Smyth 1949), and Wisconsin (Keenlyne 1972) found that dietary samples contained between 73.1 and 100% mammalian prey. Clark (2002) examined the diet of the Timber Rattlesnake throughout its range by reviewing 400 published dietary records, including records from the aforementioned studies, and dissecting 1,108 museum specimens to recover 189 prey items from the stomachs of 178 individuals. He found that mammals comprised 91.1% of the total diet. Although birds are typically the second most commonly recovered prey in dietary studies of the Timber Rattlesnake (Uhler et al. 1939; Platt et al. 2001; Clark 2002; but see Hamilton and Pollack 1955), a low frequency of arboreal activity among snakes in this study may explain the lack of birds in their diet.

As snakes increase in size, they often add larger prey to their diet (Mushinsky 1987). With this upward shift in prey size, some species exhibit a concomitant refusal to target smaller prey (Reynolds and Scott 1982; Arnold 1993; Shine and Sun 2003; but see Nowak et al. 2008; Repp and Schuett 2008). In this study, the three larger prey types (rats, rabbits, and squirrels) were in fact taken by snakes > 70.0 cm SVL. However, snakes > 80.0 cm

SVL continued to take shrews, mice, and voles. Clark (2002) and Reinert et al. (2011a) also confirmed this trend regarding the size of Timber Rattlesnakes and the prey they consume. The willingness of large Timber Rattlesnakes to take available prey, regardless of size, may contribute to the ability of this species to use a variety of habitats.

It is thought that some New World pitvipers prey on ectotherms as juveniles and later shift to endothermic prey as adults (Campbell and Lamar 2004). I examined dietary material from seven young Timber Rattlesnakes ranging between 31.0 and 66.3 cm SVL and recovered one shrew, three mice, two voles, and one unidentifiable mammal. Both voles were taken by the largest two individuals of this group (60.0 and 66.3 cm SVL). Clark (2002) found that the diet of young Timber Rattlesnakes consisted entirely of small mammalian prey.

Consistent with the findings of this study, the few reported dietary records from other Timber Rattlesnake populations using disturbed, agricultural habitats also indicate that field-dwelling voles are important prey (Fogell 2000; Fitch and Pisani 2006). In northeastern Kansas, six of 17 prey items recovered from individuals foraging in secondary woodlands, grasslands, and old fields were Prairie Voles (Fitch and Pisani 2006). Pisani and Fitch (2006) suggested that high Prairie Vole densities contributed to the rapid growth rates of some snakes in the population. In Southeastern Nebraska, Timber Rattlesnakes have been shown to leave wooded areas to forage in fields, including those planted in row-crops (Fogell 2000; Fogell et al. 2002a). Fogell (2000) reported that 13 identified prey items from this Nebraska population included one Prairie Vole and three Meadow Voles (*Microtus pennsylvanicus*).

Mammal trapping.—I captured small mammals with greater success in edge and woodland habitats than in fields. Given the degree of field use by foraging Timber Rattlesnakes in the study population, as well as the importance of Prairie Voles in their diet, low capture rates in fields were surprising. Previous studies on Timber Rattlesnakes found that individuals typically consume small mammals in proportions similar to the local abundance of those species (Reinert et al. 1984; Clark 2002). However, Reinert et al. (2011a) contradict these earlier studies and also found that vole species comprised a greater proportion of the observed diet than predicted by mammal trapping. Reinert et al. (2011a) provide possible explanations for their findings including 1) experience-based foraging preference, 2) differential catchability among rodent species, 3) trapping biases, and 4) microgeographic variation in prey densities. At my study site, it was unlikely that Prairie Voles were rare. In nearby northeastern Kansas, Fitch (1957) found that Prairie Voles were the most abundant mammal in grassland areas. Martin (1956)

stated that Prairie Voles were perhaps the most important species of mammal in the grasslands of Kansas and adjacent states. Possible explanations as to why Prairie Voles were not captured in large numbers might be explained by their dedicated use of well-established runway systems (Stokes et al. 2001) or their tendency to spend much of their time in elaborate tunnel systems, some of which are entirely below ground (Jameson 1947).

The non-folding Sherman live traps used in this study were capable of capturing medium-sized small mammals, the largest of which was an adult Cotton Rat weighing 162.5 g. Traps should have been sufficient to capture Eastern Chipmunks (*Tamias striatus*), a common prey of Timber Rattlesnakes (Clark 2002), but they were never observed or trapped at the study site. Although the traps used in this study were not sufficient to sample large squirrels and rabbits, only eight of 145 (5.5%) Timber Rattlesnakes captured in this study were truly large (exceeding 1,000 g and 100 cm SVL) and even large individuals of this species continue to take small prey (Clark 2002; Reinert et al. 2011a; this study). Therefore, I conclude that the dominant prey species were subject to sampling. Reinert et al. (2011a) reached similar conclusions regarding the use of medium-sized Sherman live traps in their study of Timber Rattlesnake foraging ecology. Nevertheless, the extent to which the habitat use patterns of larger snakes might have been influenced by squirrel and/or rabbit densities remains unknown.

Fields as ecological traps.—Annual adult survival of Timber Rattlesnakes in mature forests has been estimated at approx. 90% (Brown et al. 2007). By contrast, eight of the 26 telemetry subjects (30.8 %) in this study were found dead within two years of being implanted. Sources of mortality were known for six of the dead subjects (75%), all of which were human-induced. Four were killed by farm implements while in fields (three females, one male). One male was destroyed by a landowner when it was found in his driveway and another male was killed by a vehicle on a state highway. Additionally, each season, I found non-radio-tagged Timber Rattlesnakes dead on gravel roads surrounding the quarry.

A radio telemetry study conducted in northwestern Missouri reported that mowing resulted in a 43% mortality rate for Massasaugas (*Sistrurus catenatus*) dwelling in grasslands (Durbian 2006), but I found only an anecdotal account of Timber Rattlesnakes being killed during the haying of a Vermont dairy farm (Furman 2007). I am unaware of other studies in which radio-tagged Timber Rattlesnakes were killed by farm implements. Of the snakes killed by farm implements in this study, three were killed by mowers in grassy or old fields while the plowing of a fallow crop field resulted in

the death of a fourth individual. Behaviors at the time of death remain unknown, but these snakes were likely foraging. Unlike Timber Rattlesnakes in the Coastal Plain of South Carolina that prefer to forage in forests and primarily use fields during the mating season (Waldron et al. 2006), it was not uncommon for snakes in this study to spend much of the active season foraging in one particular field where they moved very little between successive relocations. Compared to snakes that use fields intermittently, a high degree of site fidelity increases the chance of an individual encountering a farm implement.

Fogell (2000) suggested populations in geographic regions historically containing grasslands may be predisposed to using agricultural habitats. If this assertion is correct, the same suite of structural, thermal, and resource-based cues that caused Timber Rattlesnakes to forage in native prairies might now be causing them to forage in fields with anthropogenic components. If human-induced mortality is the consequence of this formerly adaptive behavior, fields may be functioning as ecological traps (Schlaepfer et al. 2002). Theoretically, increased mortality could be offset by rapid growth, early maturation, and increased fecundity if fields provide abundant prey.

Conclusions and management implications.—Near the western edge of their geographic range where landscapes are heterogeneous and further fragmented by agriculture, Timber Rattlesnakes readily forage along habitat edges and in open fields (Fitch 1999; Fogell et al. 2002a; Fitch et al. 2004; Fitch and Pisani 2006; this study). Even within closed-canopy forests, Timber Rattlesnakes exhibit variable food habits and ambush strategies (Reinert et al. 2011a) and will use edges and clearcuts when available (Martin 1979; Adams 2005; but see Sealy 2002; Waldron et al. 2006). Such behavioral plasticity and tolerance for habitat alteration suggests that prey availability may be more important to this species than the physical structure of the habitat in which it forages. Studies indicate that Timber Rattlesnakes may be tolerant of silvicultural practices (Reinert et al. 2011b) that can increase small mammal densities (Kirkland 1977, 1990). Therefore, managing forests for high densities of small mammals may be an important strategy for maintaining viable Timber Rattlesnakes populations throughout their range (Beaupre and Douglas 2009).

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ROD D. WITTENBERG serves with the U.S. Fish and Wildlife Service as the Deputy Project Leader at Ruby Lake National Wildlife Refuge in Ruby Valley, Nevada, USA. He received a B.S. in Biology from Avila College, a M.S. in Biology from the University of Texas at Tyler, and a Ph.D. from the University of Arkansas. His interest in snake research is broad, with past and present studies focusing on systematics, foraging ecology, thermal biology, movement and habitat use, morphology and growth, road mortality, and trapping methods. (Photographed by Sara E. Wittenberg).