

## Hibernation Site Selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near Their Northern Range Limit

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**ABSTRACT.**—Hibernation sites at higher latitudes must protect snakes from colder conditions for longer periods of time. Because fewer locations are likely to be suitable, hibernation site availability may restrict the northern distribution of snakes. We considered overwinter mortality, hibernation site fidelity, and the abundance of suitable hibernation sites based on surface features to assess whether Massasauga Rattlesnakes are likely to be limited by hibernation site availability on the Bruce Peninsula, Ontario, Canada. We used three years of radio telemetry to locate 46 hibernation sites of 32 individual snakes. Snakes hibernated individually in old root systems, rodent burrows, and rock crevices in forested areas. Hibernation sites could be differentiated from forested areas generally available to snakes but not from locations with holes and crevices in the immediate vicinity of hibernation sites. Few snakes hibernated in the same location in consecutive years, although most (>70%) hibernated within 100 m of their previous location. Overwinter mortality over three years (23%) was similar to mortality during the active season (21%). Our results suggest that Massasauga Rattlesnakes may be limited by the availability of suitable hibernation sites, but sites of similar quality to those used by overwintering snakes are locally abundant. The location of hibernation sites within forests could not be predicted reliably based on surface features. Therefore, efforts to conserve habitat for this threatened species should consider all forested areas on the Bruce Peninsula as potential hibernation habitat.

Many animals use dormancy to avoid stressful environmental conditions (Danks, 1987; Guppy and Withers, 1999). For ectotherms such as snakes, hibernation can be critical for surviving temperate-zone winters because an inability to generate substantial metabolic heat can make exposure to low temperatures lethal (Gregory, 1982). At higher latitudes, long winters require that snakes spend as much time in hibernation as they spend active (e.g., Aleksiuik, 1976; Jacob and Painter, 1980; Gannon and Secoy, 1985; Larsen and Gregory, 1989; Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001a; O'Donnell et al., 2004). Because hibernacula at higher latitudes must protect snakes from colder conditions for longer periods of time, fewer locations are likely to be suitable for overwintering, possibly affecting the local abundance of snakes (Gregory, 1982). Here we assess whether hibernation sites are likely to be limiting for Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) on the Bruce Peninsula, Ontario, near the northern extent of their range.

Although direct evidence is lacking, several observations suggest hibernation sites may be limiting for northern populations. High mortality rates during hibernation (e.g., Viitanen, 1967; Blem and Blem, 1995; Shine and Mason, 2004) could reflect a scarcity of suitable hibernation sites. Many snakes return to the same hibernation sites from year to year (e.g., Woodbury et al.,

1951; Fitch, 1960; Brown, 1992; Johnson, 1995; Prior et al., 2001; Shine and Mason, 2004), which may reflect limited availability of suitable sites. Most convincingly, snakes tend to occupy fewer hibernation sites and become more communal (i.e., den) in northern climates (Gregory, 1984; Sexton et al. 1992). However, Massasauga Rattlesnakes occur near the northern limit of all north-temperate pitvipers but hibernate individually (Johnson, 1995), suggesting suitable hibernation sites are not limiting for this species. To explore this further, we considered (1) overwinter mortality, (2) hibernation site fidelity, and (3) the abundance of suitable hibernation sites based on surface features to assess whether Massasauga Rattlesnakes are likely to be limited by hibernation site availability on the Bruce Peninsula.

Eastern Massasauga Rattlesnakes are threatened by habitat loss throughout most of their range (J. Symanski, USFWS, Fort Snelling, MN, 1998). Being able to predict reliably the location of hibernation sites would be of obvious conservation utility, allowing the identification and protection of this important habitat component. Detailed descriptions of hibernation sites are lacking for the Bruce Peninsula population, although hibernation sites appear concentrated in forested areas (Weatherhead and Prior, 1992; Harvey and Weatherhead, in press). In other parts of its range, the species hibernates in crayfish burrows (Maple, 1968; Reinert, 1978; Seigel, 1986), wetland hummocks (Johnson, 1995), and rock crevices (Wright, 1941). A common feature of

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hibernation sites across the range seems to be access to the unfrozen portion of the water table (Johnson, 1995).

Few studies have attempted to characterize snake hibernacula structurally. Although the critical features of hibernation sites are likely subsurface (Costanzo, 1989), surface features might serve as a proxy for subsurface conditions (or be important in their own right). In two previous studies, hibernation sites used by snakes could be differentiated from random sites (Burger et al., 1988; Prior and Weatherhead, 1996) but not from nearby "potential" hibernation sites (Prior and Weatherhead, 1996) based on surface features (i.e., a potential hibernation site was a location looking similar to known hibernation sites). Both studies were based on relatively few hibernation sites ( $N = 7$  and  $N = 10$ , respectively) and involved snakes with fundamental differences in hibernation behavior from Eastern Massasauga Rattlesnakes: Pinesnakes (*Pituophis melanoleucus*) are capable of creating new burrows (Burger et al., 1988) and Black Ratsnakes (*Elaphe obsoleta*) are communal hibernators (Prior and Weatherhead, 1996). Our secondary objective was to determine whether hibernation sites could be reliably differentiated from nearby "potential" hibernation sites and random sites based on surface features.

#### MATERIALS AND METHODS

We conducted our research on the Upper Bruce Peninsula (50°04'N, 45°44'W), Ontario, Canada, near the northern limit of the species' distribution (Symanski, 1998). The area is characterized by shallow soil over a limestone base (Hoffman and Richards, 1954) and karstification has created subsurface openings in the limestone (Cowell and Ford, 1983).

Hibernation sites were located by tracking snakes implanted with radio transmitters (Model SI-2T, Holohil Systems Inc., Ontario, Canada). Surgical procedures generally followed Reinert and Cundall (1982). Postsurgery, snakes were held for three days and then released at the point of capture. We initially found snakes opportunistically by searching, with most subsequent captures resulting from finding other snakes near those we were tracking. We sexed snakes using cloacal probes. We classified females as gravid based on distinctive behavior during summer (extensive basking, sedentary) coupled with observations of neonates near the females in late summer. From 2001 to 2003, we implanted transmitters into 19 males, nine gravid females, and six nongravid females. Five females were gravid in one year and nongravid the next year, and one female went from nongravid to gravid between years.

We relocated snakes on average every two days through the fall until they occupied consistent underground locations, where they remained for the winter. The location of each hibernation site was recorded in Universal Transverse Mercator (UTM) coordinates (North American Datum of 1983) using a handheld global positioning system unit (GPS 12XL). No snakes were handled within a month of ingress to avoid affecting hibernation behavior; thus, body condition of snakes entering hibernation was unknown. In spring, hibernacula known to be occupied by snakes with transmitters were monitored weekly for emergence. We assumed snakes had died in hibernation if they had not emerged by midsummer and a radio signal could still be detected underground. In two cases, transmitters failed during hibernation and the fate of the snake could not be determined.

We used 20 structural variables (Table 1) derived from previous studies (Reinert, 1984; Prior and Weatherhead, 1996; Blouin-Demers and Weatherhead, 2001b; Harvey and Weatherhead, in press) to quantify microhabitat at each hibernation site. Plots were centered at the nearest apparent access point (i.e., hole or crevice) to underground locations of hibernating snakes. The percent coverage of each ground cover type was estimated from digital photos taken above each plot. We estimated percent canopy closure from two digital photos of the canopy above the snake's position using ArcView Image Analysis (v1.1).

For each hibernation (H) site we sampled two other sites: a potential hibernation (P) site, and a random (R) site. P-sites were centered on a hole or crevice within 30 m of an H-site and were used to determine whether actual hibernation sites differed from nearby habitat that looked similar. To reduce bias toward sampling readily visible openings, we located three P-sites for each H-site and randomly selected one of the three for sampling. We could not discount the possibility that P-sites were occupied by snakes. R-sites were selected 200 m from H-sites in a random direction and represented habitat generally available to snakes within forests. We quantified the same microhabitat variables at potential hibernation and random sites as at hibernation sites. At each sampling location we also identified to species the five closest trees (woody stems, > 2 m tall) because specific tree species may be associated with subsurface conditions that are favorable to hibernating snakes.

*Data Analysis.*—Prior to conducting multivariate analyses, we removed one variable from pairs of highly correlated ( $|r| > 0.7$ ) variables to reduce multicollinearity. A combination of arcsine, lognormal, square root, and cosine transformations improved the fit of each remaining variable to a normal distribution. We used

TABLE 1. Structural habitat variables used in the analysis of hibernation site selection by Eastern Massasauga Rattlesnakes on the Bruce Peninsula, Ontario from 2001 to 2003.

Variable abbreviation	Radius <sup>a</sup> (m)	Variable description
DOS	30	Distance (m) to nearest overstory tree (> 2 m tall, > 7.5 dbh <sup>b</sup> )
DUS	30	Distance (m) to nearest understory tree (> 2 m tall, < 7.5 dbh)
D5TREES	30	Mean distance (m) to nearest 5 trees
DSHRUB	30	Distance (m) to nearest shrub (< 2 m tall)
DROCK	30	Distance (m) to nearest rock (> 20 cm maximum length)
DLOG	30	Distance (m) to nearest log (> 7.5 cm maximum diameter)
DBHOS	30	Diameter at breast height (cm) of nearest overstory tree
DBHUS	30	Diameter at breast height (cm) of nearest understory tree
DBH5TREES	30	Mean diameter at breast height (cm) of nearest 5 trees
HSHRUB	30	Height (cm) of the nearest shrub
LROCK	30	Maximum length (cm) of the nearest rock
DIAMLOG	30	Maximum diameter (cm) of the nearest log
%ROCK	1	Coverage of rocks (%) within plot
%LOG	1	Coverage of logs (%) within plot
%LEAF	1	Coverage of leaf litter (%) within plot
%VEG	1	Coverage of vegetation (i.e. shrubs, grasses) (%) within plot
#WSTEMS	1	Total number of woody stems within plot
%CANCOV	0	Canopy cover (%) above plot
SLOPE	0	Maximum slope (°) at of plot
ASPECT	0	Aspect (°) of maximum slope

<sup>a</sup> Maximum distance from the center of the plot the variable was measured.

<sup>b</sup> Diameter at breast height.

principal components analysis (PCA) to reduce the dataset, retaining only significant ( $\lambda > 1$ ) principal components for further analyses. We conducted multivariate analysis of variance (MANOVA) using PCA values to test whether H-, P-, and R-sites differed. Discriminant func-

tion analysis (DFA) was used to interpret group differences. The effectiveness of DFA in distinguishing between groups was assessed using jackknife cross-validation error estimates. The statistical significance of these error estimates was assessed using randomization tests with 1000 replicates (Solow, 1990).

We used logistic regression to determine whether snakes were more likely to survive in hibernation sites with a particular microhabitat structure. We used bootstrapping with 1000 replicates to estimate variance in mortality rates and enhance the reliability of chi-square tests (Efron and Tibshirani, 1993). Statistical analyses were performed using Excel 2002, JMP 4.0.0, SPSS Version 13.0, and Systat Standard Version 11. Test statistics were considered significant at  $\alpha = 0.05$ .

## RESULTS

From 2001–2003, 46 hibernation locations were identified for 32 individual snakes (19 snakes = 1 location, 12 snakes = 2 locations, 1 snake = 3 locations). No two snakes used the same hibernation site. Snakes hibernated in old root systems, rodent burrows, and rock crevices with southern exposure (mean ASPECT:  $194^\circ \pm 17$  SE) in forested areas. Of the 44 cases where the fate of the snake could be determined, 10 snakes died during winter (mortality rate:  $23\% \pm 6$  SD). The mortality rate during the active season was similar (21%), with seven snakes dying in 2463 days of tracking (active season length approximately 184 days). Snakes that survive hibernation may emerge in poor health and die immediately after, as opposed to during, hibernation (Prior and Shilton, 1996; Dutton and Taylor, 2003). Three snakes were depredated within a week of emerging from hibernation and prior to dispersing from their hibernation site. If these deaths are considered hibernation-induced, the winter mortality rate would increase to  $30\% \pm 7$  SD and the active season mortality rate decrease to 12%.

Nonreproductive females had a lower overwinter mortality rate (one of 12, 8%) than males (six of 23, 26%) or postpartum females (three of 9, 33%) but with small sample sizes the differences were not statistically significant ( $\chi^2_2 = 2.14$ ,  $P = 0.343$ , bootstrap  $P = 0.262$ ). Overwinter mortality was more than twice as high in 2003 (six of 14, 43%) as in 2002 (two of 18, 11%) or 2001 (two of 12, 17%), but differences were not statistically significant ( $\chi^2_2 = 4.86$ ,  $P = 0.088$ , bootstrap  $P = 0.142$ ).

Few snakes occupied the same hibernation site in consecutive years, although most hibernated within 100 m of their previous location (Fig. 1). One snake hibernated in three different locations

in three consecutive years, with sites (on average) 288 m from one another.

The closest tree to a hibernation site was either an Eastern White cedar (*Thuja occidentalis*, 40%), another coniferous tree (*Abies balsamea*, *Larix laricina*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, 37%), or a deciduous tree (six species, 23%). The five trees closest to each hibernation site were also Eastern White cedars (50%), other coniferous trees (29%), and deciduous trees (21%). Neither of these compositions differed significantly from those at P- or R-sites (closest tree  $\chi^2_4 = 2.43$ ,  $P = 0.657$ , bootstrap  $P = 0.317$ ; closest five trees  $\chi^2_4 = 5.05$ ,  $P = 0.282$ , bootstrap  $P = 0.190$ ).

We sampled the microhabitat structure of 30 H-, 30 P-, and 30-R sites. The H-sites were used by 28 individual snakes, and the multiple sites used by the same snake were > 250 m apart. We eliminated from subsequent analyses the variables %LEAF and D5TREES due to high correlation with other variables (%VEG and DUS, respectively). PCA reduced the remaining dataset to seven significant principal components that explained 68% of the variation in habitat structure among all sites. Microhabitat at H-, P-, and R-sites did not differ significantly ( $\Lambda = 0.78$ ,  $F_{14,162} = 1.51$ ,  $P = 0.113$ ), although microhabitat differences between H- and R-sites approached significance ( $F_{7,81} = 2.09$ ,  $P = 0.054$ ). A single discriminant function explained most (69%) of the variation between groups, and a single principal component (PC5) was strongly correlated ( $r = 0.81$ ) with that discriminant function (all other PC/DF correlations < |0.21|). Principal component 5 described a gradient of increasing vegetation cover (%VEG), rock length (LROCK), and shrub height (HSHRUB). Repeating analyses with only these three variables revealed significant differences between microhabitat at H-, P-, and R-sites ( $\Lambda = 0.76$ ,  $F_{6,170} = 4.11$ ,  $P = 0.001$ ). Interpreting the first discriminant function (which accounted for 98% of the variation among groups), H- and P-sites had a higher percentage of vegetation cover, larger rocks, and taller shrubs than R-sites (Fig. 2). H sites were (on average) 0.3 m from the nearest shrub and 1.5 m from the nearest rock. The likelihood of a snake surviving hibernation was not related to microhabitat structure ( $\chi^2_1 = 0.43$ ,  $P = 0.514$ ).

Upon cross-validation, 18 of H-sites, seven of P-sites, and 19 of R-sites were correctly classified (44 of 90 overall, 49%). If group membership were to be randomly assigned to observations, only 33% on average would be correctly classified by discriminant analysis (randomization  $P < 0.001$ ). Therefore, H-sites could be weakly differentiated from P- and R-sites based on microhabitat structure.

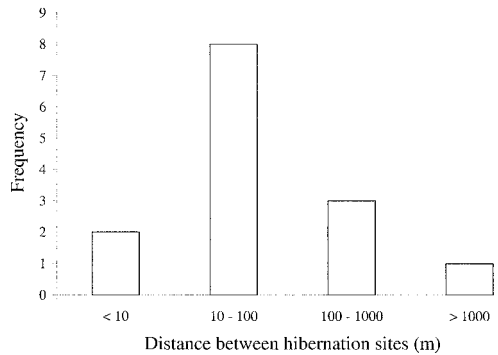


FIG. 1. A frequency histogram of distances between hibernation sites used in consecutive years by Eastern Massasauga Rattlesnakes on the Bruce Peninsula, Ontario from 2001 to 2003.

#### DISCUSSION

Eastern Massasauga Rattlesnakes on the Bruce Peninsula hibernated individually in old root systems, rodent burrows, and rock crevices in forested areas. Hibernation sites usually faced south, but that was also true of P- and R-sites. Southern aspect could be an important feature of hibernation sites, but our random sampling was too close to hibernation sites to identify this as a feature specific to them. Southern exposure is a common feature of north-temperate hibernation sites (e.g., Carpenter, 1953; Drda, 1968; Macartney et al., 1989; Brown, 1991; Prior and Weatherhead, 1996) and presumably functions either to moderate subterranean temperatures or facilitate warming during emergence in the spring. Almost all hibernation sites identified on the Bruce Peninsula have been in forests (Weatherhead and Prior, 1992; Harvey and Weatherhead, in press; this study). In contrast, Massasauga Rattlesnakes in more southern latitudes hibernate in open-canopy wetlands (Wright, 1941; Maple, 1968; Reinert and Kodrich, 1982; Johnson, 1995). The geographical difference is clear, but the causal explanation awaits further ecophysiological work.

A substantial percentage of snakes (11–43% annually) died while hibernating each year, similar to the highest rates of overwinter mortality reported for snakes (18–47% Viitanen, 1967), excluding catastrophic events (e.g., Shine and Mason, 2004). The mortality rate would be slightly higher if the three snakes depredated within a week of emergence were considered cases of overwinter mortality (e.g., if snakes emerge from hibernation in such poor health that predation was likely). Alternatively, snakes may emerge in good health but with low body temperatures. Lower body temperatures could increase a snake's likelihood of predation by reducing its ability to fight or flee (Angilletta et al.,

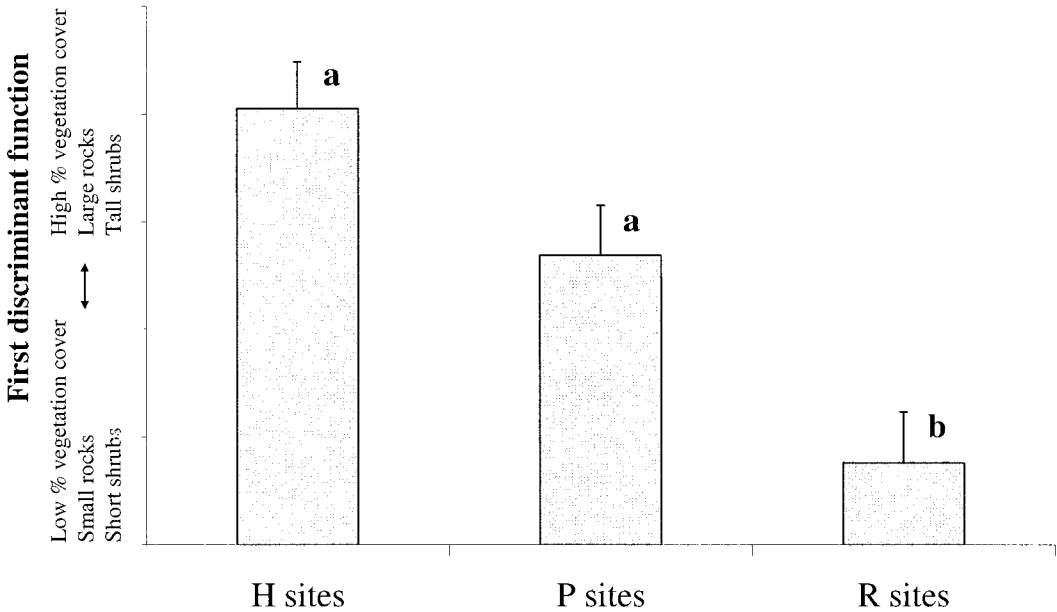


FIG. 2. Mean ( $\pm$  SE) discriminant function scores of hibernation (H), potential hibernation (P), and random (R) microhabitat for Eastern Massasauga Rattlesnakes on the Bruce Peninsula, Ontario from 2001 to 2003. A common lowercase letter above bars indicates groups were not significantly different (F test with 3 and 85 degrees of freedom,  $P > 0.05$ ).

2002) or by increasing basking behavior. We did not assess the body condition of snakes upon emergence and, thus, were unable to distinguish between these alternatives. Combining active season and overwinter mortality, only about 60% of snakes survived from one year to the next. Given low annual survivorship and the intermittent reproduction of northern crotalids (Reinert, 1981; Brown, 1991; Holycross and Goldberg, 2001), most females would be unlikely to survive more than 2–3 reproductive episodes. This may have important life-history consequences in terms of investment in early reproduction (Shine, 2003).

High rates of overwinter mortality suggest Massasauga Rattlesnakes are limited by the availability of suitable hibernation sites. Snakes may perish in unsuitable sites by freezing (Shine and Mason, 2004), starvation (Aleksiuk and Stewart, 1971), or dehydration (Costanzo, 1989). However, overwinter mortality could also be caused by factors unrelated to the inherent quality of a site, such as predation, disease, parasitism, and extreme weather events (e.g., flooding). Because we could not excavate hibernation sites to determine the proximate causes of mortality for hibernating snakes, we were unable to confirm overwinter mortality was caused by hibernating in unsuitable sites.

Few snakes hibernated in the same location in consecutive years, but most hibernated in the

same general area as previous years. Massasauga Rattlesnakes at Cicero Swamp, New York, also returned to the same general area to hibernate in consecutive years but rarely used the same specific site (Johnson, 1995). Studies reporting high rates of hibernation site fidelity have all been based at dens (Woodbury et al., 1951; Fitch, 1960; Parker and Brown, 1973; Prior et al., 2001; Shine and Mason, 2004). This is not surprising, because both hibernation site fidelity and communal hibernation are expected responses to low hibernation site availability (Gregory, 1984). Individual hibernation and fidelity to a general area (but not a specific hibernation site) in Massasauga Rattlesnakes suggest hibernation sites are locally abundant but restricted at a landscape scale. This interpretation is supported by the fact that P-sites (within 30 m of actual hibernation sites) were indistinguishable from H-sites based on surface features, whereas R-sites (200 m from actual hibernation sites) could be differentiated from H- and P-sites. Assuming surface features are related to the suitability of a site for overwintering, equally suitable hibernation sites were available in the immediate vicinity of actual hibernation sites. Viitanen (1967) reached a similar conclusion about the distribution of *Vipera berus* hibernation sites in Finland.

Snakes hibernated in locations with abundant vegetative ground cover, tall shrubs, and large

nearby rocks. Association of hibernation sites with abundant vegetation has also been noted in Pinesnakes (Burger et al., 1988) and Massasauga Rattlesnakes in Pennsylvania (Reinert and Kodrich, 1982). Vegetation cover may protect hibernation sites from extreme weather conditions or moderate daily temperature fluctuations (Geiger, 1965; Burger et al., 1988). A similar function could be argued for the presence of large rocks, which moderate surface temperatures to a greater extent than smaller rocks (Huey et al., 1989). This would be particularly important for snakes near their northern range limits that encounter challenging weather conditions during hibernation. Alternatively, surface associations may simply correlate with other features that determine the location of hibernation sites. For example, sub-surface conditions promoting shrublike vegetative growth (e.g., moist, shallow, rocky soils) could be ideal for hibernating snakes. Critical internal features of hibernation sites could include the following: (1) structural stability (Prior and Weatherhead, 1996); (2) access to the water table (Carpenter, 1953; Maple, 1968; Reinert, 1978; Johnson, 1995); (3) depth below the frost line (Bailey, 1949); and (4) space within sites to adjust to changing conditions (Sexton and Marion, 1981).

Viewed collectively, our results suggest that Massasauga Rattlesnakes on the Bruce Peninsula may be limited by the availability of suitable hibernation sites, but sites of similar quality to those used by overwintering snakes are locally abundant. Within areas containing hibernation sites used by snakes, karstification likely increases the number of available sites by creating more underground spaces. Other studies have produced results consistent with (e.g., Shine and Mason, 2004) and contrary to (e.g., Viitanen, 1967; Lang, 1971; Prior and Weatherhead, 1996) the hypothesis that hibernation site availability limits the northern distribution of snakes. The leading alternative hypothesis is that the active season becomes too short for successful reproduction at northern latitudes (Bartlett, 1976; Peterson et al., 1993). These hypotheses are not mutually exclusive. A short active season at northern latitudes may be sufficient for females to gestate but allow little time postpartum to forage prior to hibernating. If snakes enter hibernation in an emaciated state as a result, fewer locations are likely to be suitable for overwintering. Whether Massasauga Rattlesnakes are limited by the length of the active season on the Bruce Peninsula remains to be determined.

In recommending conservation steps, reserves designed to protect Massasauga Rattlesnakes on the Bruce Peninsula should include forested habitat to protect its hibernation sites. The precise location of hibernation sites within forests cannot

be predicted reliably based on surface features. However, the clustering of hibernation sites in certain areas suggests features at a landscape scale (e.g., southern exposure) may indicate whether areas are more or less likely to contain hibernation sites. Until such analyses are performed, a useful initial approach would be to consider all forested areas on the Bruce Peninsula as potential hibernation habitat, with an objective of protecting as much of this habitat as possible. If it is necessary to identify actual hibernation sites, radio telemetry remains the most reliable approach.

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## Effects of Different Burn Regimes on Tallgrass Prairie Herpetofaunal Species Diversity and Community Composition in the Flint Hills, Kansas

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**ABSTRACT.**—The Flint Hills region of Kansas is the largest contiguous area of tallgrass prairie remaining today. Historically, the tallgrass prairie burned every 2–3 yr on average, but current land managers have altered burn regimes, resulting in a range of habitats from annually burned to long-term unburned. We used drift fence/funnel trap arrays and coverboards to estimate species richness, evenness, and diversity of herpetofauna within three different burn regimes: annual, 4-yr, and long-term unburned at Konza Prairie Biological Station, Riley County, Kansas. During the spring and fall of 2003–2004, 315 individuals from 20 species were captured across all burn regimes. Herpetofaunal species richness, evenness, and diversity estimates were not different between the three burn treatments. However, because of species-specific responses to individual burn regimes, community composition was significantly different between the habitats ( $\chi^2 = 158.19$ ,  $df = 20$ ,  $P < 0.001$ ). Four species exhibited preferences among burn regimes, which differed significantly from independent assortment, with *Eumeces obsoletus* and *Phrynosoma cornutum* preferring annual burn treatments, *Scincella lateralis* preferring 4-yr burn treatments, and *Diadophis punctatus* preferring long-term unburned treatments. Species-specific responses were likely because of changes in vegetation structure and microhabitat (temperature and moisture content) created through different frequencies of fire disturbances. Maximizing large-scale herpetofaunal diversity across the Flint Hills' rangelands could be accomplished by creating a large number of small scale habitat types through a mosaic style burning plan.

Fire is an essential component in the development and persistence of the tallgrass prairie ecosystem (Axelrod, 1985). Regular burning of tallgrass prairie increases plant productivity

(Briggs and Knapp, 1995), decreases above-ground litter (Hulbert, 1988), and decreases woody vegetation (Heisler et al., 2003). The Flint Hills encompass over 1.6 million ha extending throughout much of eastern Kansas from near the Kansas-Nebraska border south into north-eastern Oklahoma and contain the largest re-

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maining area of unplowed tallgrass prairie in North America. Ranchers throughout the Flint Hills practice prescribed burning. However, the frequency at which the prairie is burned varies depending upon management practices of individual ranchers. The spatial, and in some cases temporal, extents to which these burns are carried out differ noticeably from historical fire regimes of the area (Anderson, 1990). Historically, tallgrass prairie burned every 1–5 yr (Collins and Gibson, 1990), which is an average of approximately 2–3 fires every 5 yr. Recent human land-use altered this frequency in various directions (Briggs et al., 2002). Annually burned rangelands became prevalent in the early 1980s because of a switch in cattle grazing practices from traditional season-long to early-intensive stocking (Robbins et al., 2002), whereas land in close proximity to developed areas remained unburned for long periods of time (> 20 yr).

Various fire regimes result in differences in ground cover, refuges (Hulbert, 1988), potential prey species (Clark and Kaufman, 1990), temperatures (Knapp and Seastedt, 1986), moisture levels (Blair, 1997), and other important ecological variables. One can consider habitats created by different fire regimes as a continuum within the tallgrass prairie ecosystem, with both extremes tending toward homogeneity. Annually burned areas are dominated by  $C_4$  grasses. As time since last burn increases, shrub islands of roughleaf dogwood (*Cornus drummondii*) and smooth sumac (*Rhus glabra*) grow larger, leading to an increase in woody vegetation. Intermediate burn frequencies (2–10 yr) form habitats with different proportions of warm-season  $C_4$  grasses and woody vegetation, while long-term unburned sites are at the beginning of domination by woody vegetation (Heisler et al., 2003).

Past studies in many different ecosystems indicate that presence of fire affects community composition and species abundances either directly (e.g., mortality caused by fire), or indirectly (e.g., postfire habitat changes). There is abundant literature on the effects of fire on some animal species inhabiting tallgrass prairie, including small mammals (Clark and Kaufman, 1990; Kaufman et al., 1990; McMillan et al., 1995), birds (Zimmerman, 1992, 1993, 1997), and arthropods (Evans et al., 1983; Evans, 1984, 1988a,b; Seastedt, 1984). Changes in herpetofaunal communities caused by fire disturbances have been reported in deserts (Fyfe, 1980), forests (McLeod and Gates, 1998; Bury, 2004), tropical forests (Fredericksen and Fredericksen, 2002), savannas (Braithwaite, 1987; Hannah and Smith, 1995), and spinifex grasslands (Masters, 1996; Pianka, 1996). However, few studies have been conducted on herpetofauna in tallgrass prairie (Heinrich and Kaufman, 1985; Busby et al., 1994;

Busby and Parmelee, 1996), and fewer studies have investigated the effects of fire on herpetofauna inhabiting the tallgrass ecosystem (Cavitt, 2000; Setser and Cavitt, 2003). These latter studies examined reptile abundance preburn versus postburn (Cavitt, 2000), and snake abundance within annual and long-term unburned areas (Setser and Cavitt, 2003). The current study includes an intermediate burn frequency and multiple animal groups (anurans, turtles, snakes, and lizards). The intermediate burn frequency (in this case a 4-yr frequency) represents the historic burn regime and thus considerable portions of the management practices within the tallgrass prairie.

We hypothesized that community composition and species diversity would differ between annual, intermediate, and long-term unburned treatments. Because intermediate burn frequencies contain a mixture of woody vegetation and grasses creating many different microhabitats, we predicted that this area would contain the greatest number of species. Postfire habitats in annually burned areas can be very stressful on animal populations, so they were predicted to contain the fewest number of species and long-term unburned areas were predicted to have intermediate numbers in species.

#### MATERIALS AND METHODS

*Study Site.*—Herpetofaunal surveys were conducted during spring and fall 2003–2004 at the Konza Prairie Biological Station (KPBS; Fig. 1), located in the Flint Hills region of northeastern Kansas (39°05'N, 96°35'W). KPBS is a 3847-ha tallgrass prairie preserve owned by the Nature Conservancy and Kansas State University (KSU) and managed for ecological research by the KSU Division of Biology.

Vegetation on KPBS is dominated by a matrix of perennial, warm-season  $C_4$  grasses and a highly diverse mixture of other less abundant forb and woody species (Kuchler, 1967; Freeman and Hulbert, 1985; Freeman, 1998; Hartnett and Fay, 1998). Average monthly temperatures at KPBS range from a January low of  $-2.7^{\circ}\text{C}$  to a July high of  $26.6^{\circ}\text{C}$ . Average annual total precipitation is 835 mm with 75% falling during the growing season (Bark, 1987). Limestone outcrops are common along slopes and hilltops (Oviatt, 1998), providing shelter and habitat for much of the herpetofauna of the area.

KPBS is divided into 60 watershed units (average size =  $0.55\text{ km}^2$ ; Fig. 1), each of which is subjected to a specific burn treatment (burned at 1-, 2-, 3-, 4-, 10-, and 20-yr intervals). Trapping occurred in six different watersheds of three different burn treatments, including two annual (AB), two 4-yr (FYB), and two long-term un-

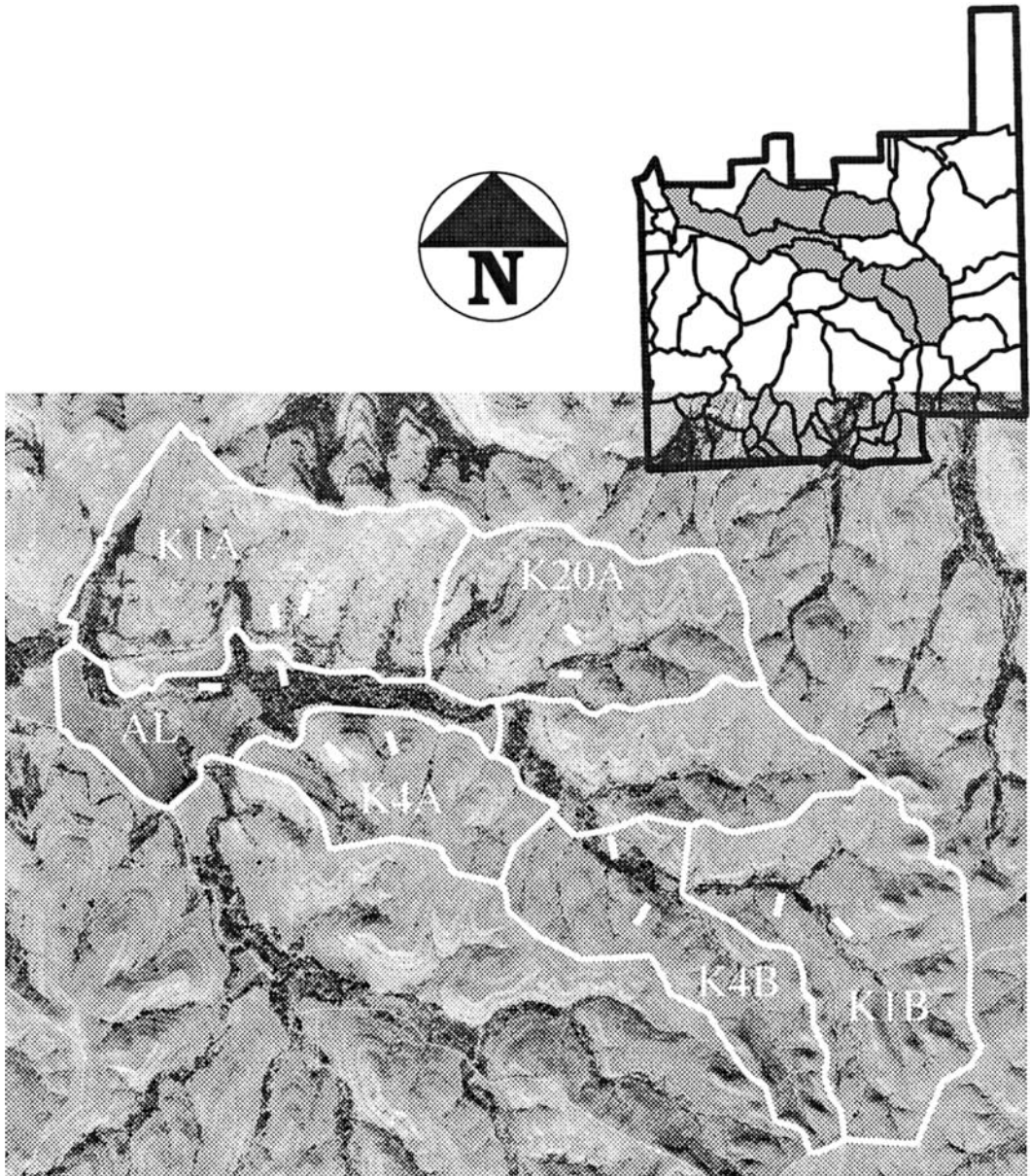


FIG. 1. Map of Konza Prairie Biological Station (KPBS). Gray shaded areas denote the watersheds used for herpetofaunal surveys during 2003–2004. White lines within watersheds indicate placement of trapping transects within burn treatments on KPBS. Two transects were placed within each of six watersheds, two of each of the three different burn frequencies. K1A and K1B = Annual burn treatment, K4A and K4B = 4-yr burn treatment, K20A and AL = Long-term unburned treatment.

burned (LTU) watersheds (Fig. 1). The AL watershed is burned on a variable schedule. However, our trap sites were located in the gallery forest portion of the watershed, which rarely burns because of low amounts of fuel on the forest floor. Thus, trap sites at this location were representative of a long-term unburned area.

*Field Protocol.*—Surveys consisted of two y-trap arrays 75 m apart, with a line of evenly spaced coverboards, two large ( $122 \times 122 \times 1.2$  cm) and three small ( $30 \times 40 \times 1.2$  cm) between (Fig. 2A). Y-trap arrays (Fig. 2B) consisted of three 16 m drift fence arms (30 cm tall) made of plastic woven geotextile silt fence, connected at the

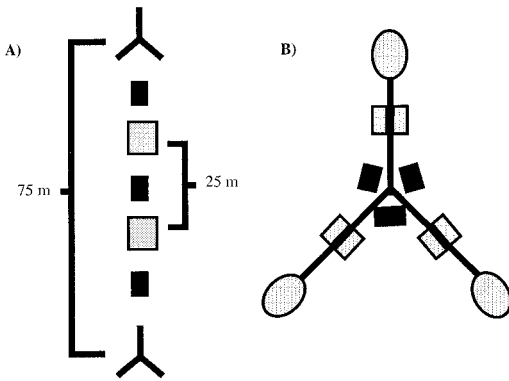


FIG. 2. Sampling methods for herpetofaunal surveys. (A) Trap transect with two y-trap arrays, one on each end. Gray squares represent large coverboards ( $122 \times 122 \times 1.2$  cm), black rectangles represent small coverboards ( $30 \times 40 \times 1.2$  cm). (B) Y-trap array design. Thatched ovals represent large collapsible funnel traps ( $68 \times 48 \times 20$  cm), thatched rectangles represent small collapsible funnel traps ( $24 \times 24 \times 40$  cm), solid rectangles represent small coverboards ( $30 \times 40 \times 1.2$  cm).

middle, and held tight to the ground by wooden stakes and bolts. Three large collapsible mesh funnel traps ( $68 \times 48 \times 20$  cm) were located at the end of each arm. Six small collapsible mesh funnel traps ( $24 \times 24 \times 40$  cm) were situated one to each side of the fence, in the middle of each arm. Three small coverboards ( $30 \times 40 \times 1.2$  cm) were located in each fork of the y-trap array. All coverboards were made from oriented strand board (OSB) plywood. Two transects were placed within each watershed (Fig. 1) for a total of 36 traps and 22 boards per watershed. Traps and boards were open 24 h/day and checked daily until daytime temperatures reached  $32^{\circ}\text{C}$ . A funnel trap day (ftd) was defined as any 24-h time period in which animals could enter a single trap. A board day (bd) was defined as any 24-h time period in which animals could shelter beneath the board. Both measurements were combined using the general notation of trap day (td).

Watersheds were sampled as two replicate sets of the three burn treatments. Each set contained one replicate of each of the three burn treatments (Set 1 = K1B, K4B, K20A; Set 2 = K1A, K4A, AL). During 2003, traps in each set were open for alternating five-day periods, whereas all sets were open simultaneously in 2004. Trapping began in spring 2003 on 21 April for set 1 and 30 May for set 2, and ended 23 June. Fall 2003 trapping began on 5 September and ended on 15 October. Spring 2004 started on 9 April for set 2 and 3 June for set 1, and ended 28 June. Fall 2004 trapping began on 16 September for

set 2 and 22 September for set 1, and trapping ended on 17 October. Across both years, set 2 was open 25 days longer than set 1 (Set 1 = 115 days, Set 2 = 140 days).

Captured animals were identified to species and individually marked if possible. Larger snakes (*Thamnophis sirtalis*, *Coluber constrictor*, *Lampropeltis triangulum*, *Lampropeltis getula*, *Elaphe emoryi*, and *Pituophis catenifer*) were marked by clipping ventral scales (Brown, 1976). Smaller snakes (*Diadophis punctatus*, *Storeria dekayi*, *Tropidoclonion lineatum*, and *Carphophis vermis*), lizards, and anurans were not marked. However, individuals of *S. dekayi*, *T. lineatum*, *C. vermis*, *Eumeces obsoletus*, *Ophisaurus attenuatus*, and all anuran captures could be analyzed for recaptures caused by low numbers of individuals caught, and site of each capture caused by nonmovement. Snout-vent length (cm) and mass (g) were recorded for each individual. Species identification and trap or board location were recorded for all animals whether or not they were handled.

**Statistical Analysis.**—Species diversity was evaluated using count data and Shannon's Index (Shannon and Weaver, 1949), which works well for nonparametric data with small sample sizes and rare species occurrences.

Comparisons between burn frequencies were performed using four estimators: (1) species richness; (2) Shannon's index ( $H$ ); (3) Shannon's equitability index ( $E_H$ ); and (4) number of individuals. Because of the short time frame of this study (2 yr), we did not have enough yearly replicates to address annual variation in activity patterns related to weather. However, analyzing data by season may be biologically meaningful because of fundamental differences in herpetofaunal behavior between spring and fall. So estimates were compared between watersheds and seasons, pooling across years. Species richness estimates were equated across all watersheds by multiplying the number of td sampled in the least sampled watershed divided by number of td sampled in the most sampled watershed. Comparisons were made using one-way ANOVA with equal samples via STATISTICA statistics software (Statsoft Inc., Tulsa, OK).

Community composition was analyzed using categorical data analysis. The Pearson chi-square test was used to test for independence of response of a species to different burn treatments. Because many species were rarely captured, the proportion of cell counts  $> 5$  was 22%. Agresti (1996) warns of possible biases in the results when  $< 25\%$  of the cell counts  $> 5$ . Therefore, different tables were created, the first included all species detected regardless of number captured, and the second included only those species with total captures across all burn frequencies  $> 5$ , resulting in 42% of the cells with counts  $> 5$ . However,

Pearson chi-square values from both were extremely large and had the same outcome; hence, inferences hereafter will refer to the table containing all 20 species captured. In an additional, post hoc analysis of the data, groups of species consisting of all anurans and small snakes specializing on earthworms were tested a second time. The Pearson chi-square statistic was calculated using SAS (version 8.0, SAS Institute, Cary, NC).

Similarity between communities in different burn treatments was assessed using Jaccard's similarity indices (JSI; Pielou, 1984) and adjusted residuals. Adjusted residuals were calculated to identify which cells violated independence (Agresti, 1996). A positive residual indicates more observed individuals than expected in the area, whereas a negative residual indicates fewer observed individuals in the area than expected. A species with a large negative residual for a specific habitat may be avoiding that habitat. Adjusted residuals  $> |3|$  for an individual species are in clear violation of independence between samples, whereas adjusted residuals  $> |2|$  are a possible rejection of independence. Adjusted residuals for the table were calculated using SAS (version 8.0, SAS Institute, Cary, NC). Significance testing was performed using a chi-square test on any species containing an adjusted residual of  $> |2|$  in any burn treatment.

Significance testing between trap types (traps and coverboards) and seasons were performed using two-sample paired *t*-tests. Trap types and seasons for each watershed were paired together (i.e., K1B boards vs. K1B traps, or K1B spring vs. K1B fall) across all watersheds to compute the mean and variance. Analysis of size differences between individuals of *D. punctatus* (the most numerous species captured) was performed using a one-way ANOVA. Alpha was set at 0.05. For all other statistical tests, because the capture data were used multiple times, we adjusted alpha to 0.01 using Bonferroni's correction.

## RESULTS

Seventeen of the 29 species that have been reported to occur on KPBS (Heinrich and Kaufman, 1985) were captured, plus an additional three species previously unrecorded: *Bufo americanus*, *S. lateralis*, and *S. dekayi*.

Summing across trap sets and years, the study consisted of 27,540 individual funnel trap days (ftd) and 16,830 individual board days (bd). A total of 315 individuals, including 21 recaptures, representing 20 species were captured (Appendix 1).

Results from different survey methods (boards and traps) differed across the study. Coverboards were seven times more efficient than funnel traps, detecting 242 individuals (mean = 0.014

ind./bd, SE < 0.001,  $N = 12$ ) when compared to the low trap efficiency of 54 individuals (mean = 0.002 ind./ftd, SE < 0.001,  $N = 12$ ) resulting in significantly more individuals per trap day detected by cover boards across all burn frequencies within each season ( $t = 4.78$ ,  $df = 11$ ,  $P < 0.001$ ). For all burn treatments, cover boards were almost twice as efficient, detecting 15 total species (mean = 0.003 sp/bd, SE < 0.001,  $N = 12$ ) compared to trap captures of 13 total species (mean = 0.001 sp/ftd, SE < 0.001,  $N = 12$ ;  $t = 4.79$ ,  $df = 11$ ,  $P < 0.001$ ). Four species were captured only in traps, whereas nine species were only captured under boards. These species would be missed if only one trap type was used.

*Species Diversity.*—Overall species richness (SR) was generally higher in annually burned (SR = 15) and long-term unburned areas (SR = 14), than 4-yr burn treatments (SR = 9). However, high variability existed between watershed-replicates of the same burn frequency (Fig. 3). Number of species captured within each burn frequency was not significantly different for either season when pooling across years (Spring:  $F = 0.56$ ,  $df = 3$ ,  $P = 0.620$ ; Fall:  $F = 0.02$ ,  $df = 3$ ,  $P = 0.982$ ). Species capture rates were slightly higher, though nonsignificant, in fall (mean = 0.11 sp/td) than in spring (mean = 0.08 sp/td;  $t = 1.92$ ,  $df = 6$ ,  $P = 0.113$ ). However, because of the shorter fall season, total species richness estimates over the entire season were similar to those of spring.

Estimates of species evenness showed similar patterns to those of species richness (Fig. 3). Species evenness estimates were higher in annually burned areas ( $E_H = 85.1$ ) when compared to 4-yr burn treatments ( $E_H = 59.7$ ) and long-term unburned areas ( $E_H = 67.5$ ). Low evenness estimates in the 4-yr frequency may have been caused by a high proportion (63%) of total captures within one species (*S. lateralis*). However, because of insufficient replication and variability within replicates, evenness was not significantly different between burn treatments for either season (Spring:  $F = 6.52$ ,  $df = 3$ ,  $P = 0.081$ ; Fall:  $F = 2.69$ ,  $df = 3$ ,  $P = 0.215$ ). When pairing estimates for each watershed, the fall season (mean = 85.98) had moderately higher estimates of evenness among captures than the spring season (mean = 69.98) across all burn treatments (Fig. 3;  $t = 2.88$ ,  $df = 6$ ,  $P = 0.035$ ).

Species diversity indices include measures of species richness and relative abundances (evenness), thus patterns in diversity estimates were similar to those already discussed. Annually burned areas showed the highest diversity when pooling across all seasons and watersheds (AB  $H = 3.3$ , FYBH = 1.9, LTU  $H = 2.6$ ). Results were inconsistent across watersheds of the same burn treatment for years and seasons creating high variability (Fig. 3); hence, Shannon diversity in-

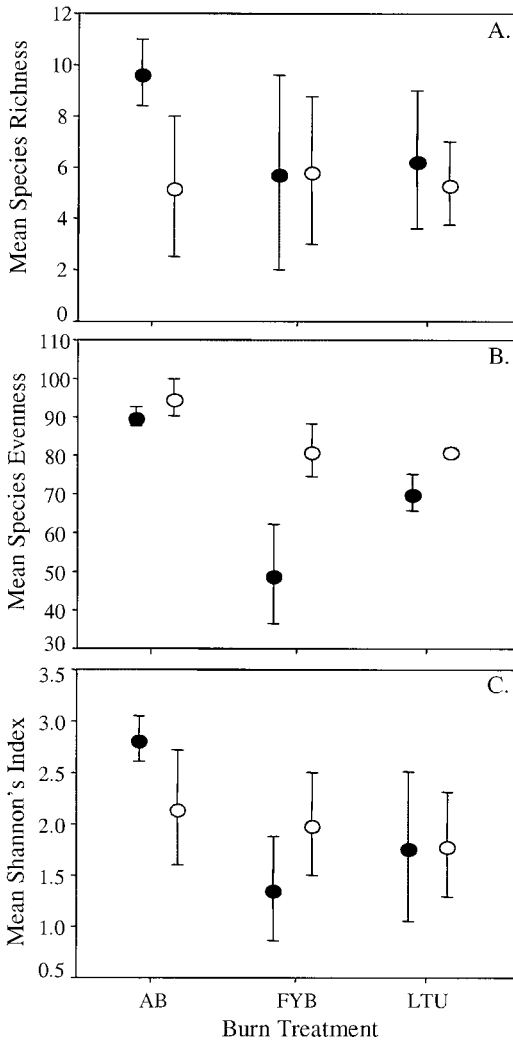


FIG. 3. Herpetofaunal community parameters estimated within different burn treatments for spring (●) and fall (○). All estimates were averaged across watersheds of similar burn treatment. Error bars represent  $\pm 1$  SE. (A) Species richness estimates for each burn treatment pooled across years within both seasons. Estimates are averages of direct counts of the number of species detected for both years. Unequal sampling efforts were equilibrated by multiplying the number of days sampled in least sampled watershed divided by the number of days sampled in most sampled watershed. (B) Species evenness ( $E_H$ ) estimates for each burn treatment pooled within each season across both years. Estimates were calculated using Shannon's evenness index. (C) Species diversity estimates ( $H$ ) for each burn treatment pooled within each season across both years. Diversity estimates were calculated using Shannon's index. AB = Annually burned, FYB = 4-yr burn, LTU = Long-term unburned.

Species richness estimates were not significantly different between burn frequencies for either season when pooling across years (Spring:  $F = 2.05$ ,  $df = 3$ ,  $P = 0.275$ ; Fall:  $F = 0.12$ ,  $df = 3$ ,  $P = 0.893$ ). Estimates of species diversity also did not differ between seasons when watershed estimates were combined (Spring  $H = 1.97$ , Fall  $H = 1.98$ ;  $t = 0.029$ ,  $df = 6$ ,  $P = 0.98$ ).

**Community Composition.**—Although overall species diversity and total abundance were relatively similar between different burn treatments, Jaccard's similarity indices (JSI) indicated that many species were not shared between different burn treatments. Indices for both seasons differed with more species being shared between treatments during spring than fall. However, patterns within burn treatment remained constant between seasons. Habitats closer to each other on the burn continuum shared more species than those further apart. Annually burned areas were more dissimilar to long-term unburned sites (Spring JSI = 0.70; Fall JSI = 0.27) than they were to 4-yr burn treatments (Spring JSI = 1.0; Fall JSI = 0.50), which were in turn more similar to long-term unburned sites (Spring JSI = 0.86; Fall JSI = 0.57).

Analysis of species captures pooled across all watersheds (Appendix 1) within burn treatments rejects independence of species captures and burn frequency ( $\chi^2 = 158.19$ ,  $df = 20$ ,  $P < 0.001$ ); thus, some species captured exhibit preferences for one of the different habitats created. The adjusted residuals for each species within a burn treatment (Table 1), suggest that some species may exhibit a positive response to specific burn treatments, whereas other species exhibit a negative response. Only one of five anuran species showed significant habitat preferences. *Gastrophryne olivacea* ( $\chi^2 = 7.0$ ,  $df = 2$ ,  $P = 0.03$ ) exhibited marginal preferences for annually burned areas and avoidance of 4-yr burn areas. Three of four lizard species exhibited significant preferences among habitats. *Eumeces obsoletus* ( $\chi^2 = 16.63$ ,  $df = 2$ ,  $P < 0.001$ ) and *P. cornutum* ( $\chi^2 = 34.00$ ,  $df = 2$ ,  $P < 0.001$ ) were found in much greater numbers in annually burned areas than would be expected if habitat choice was independent of burn regime. *Scincella lateralis* ( $\chi^2 = 63.75$ ,  $df = 2$ ,  $P < 0.001$ ) was found in much higher numbers in 4-yr burn treatments. There is also a clear avoidance of annually burned areas for this species and low numbers were found in long-term unburned areas.

The small snake, *Diadophis punctatus*, also exhibited significant habitat preferences ( $\chi^2 = 11.53$ ,  $df = 2$ ,  $P = 0.003$ ), being found in much higher numbers than expected in long-term unburned areas, and in fewer numbers in areas of higher burn frequencies. *Diadophis punctatus* was the only species with sufficient captures to

TABLE 1. Adjusted residuals of  $\chi^2$ -table for independence of herpetofaunal communities in habitats of different burn frequencies.

Common name (Scientific name)	Preference	Burn frequency			P*
		AB	FYB	LTU	
<b>Amphibians</b>					
Northern Cricket Frog ( <i>Acris crepitans</i> )		1.4	-1.4	0.1	—
Western Chorus Frog ( <i>Pseudacris triseriata</i> )		-0.7	-0.8	1.5	—
Plains Leopard Frog ( <i>Rana blairi</i> )		2.1 <sup>□</sup>	-1.1	-0.9	0.14
American Toad ( <i>Bufo americanus</i> )		1.5	-0.8	-0.7	—
Great Plains Narrowmouth Toad ( <i>Gastrophryne olivacea</i> )	AB	2.8 <sup>□</sup>	-2.0 <sup>□</sup>	-0.7	0.03
<b>Reptiles</b>					
Ornate Box Turtle ( <i>Terrapene ornata</i> )		2.1 <sup>□</sup>	-0.6	-1.4	0.15
Ground Skink ( <i>Scincella lateralis</i> )	FYB	-5.7 <sup>■</sup>	7.9 <sup>■</sup>	-2.7 <sup>□</sup>	<0.01
Great Plains Skink ( <i>Eumeces obsoletus</i> )	AB	4.5 <sup>■</sup>	-2.2 <sup>□</sup>	-2.2 <sup>□</sup>	<0.01
Texas Horned Lizard ( <i>Phrynosoma cornutum</i> )	AB	6.4 <sup>■</sup>	-3.4 <sup>■</sup>	-2.8 <sup>□</sup>	<0.01
Slender Glass Lizard ( <i>Ophisaurus attenuatus</i> )		-0.7	-1.1	2.0 <sup>□</sup>	0.37
Ringneck Snake ( <i>Diadophis punctatus</i> )	LTU	-1.3	-3.2 <sup>■</sup>	4.7 <sup>■</sup>	<0.01
Brown Snake ( <i>Storeria dekayi</i> )		-2.0 <sup>□</sup>	0.3	1.7 <sup>□</sup>	0.10
Lined Snake ( <i>Tropidoconion lineatum</i> )	AB	2.6 <sup>□</sup>	-1.4	-1.1	0.05
Western Worm Snake ( <i>Carphophis vermis</i> )		-0.7	-0.8	1.5	—
Common Garter Snake ( <i>Thamnophis sirtalis</i> )		-0.5	-1.8	2.4 <sup>□</sup>	0.07
Eastern Yellow-bellied Racer ( <i>Coluber constrictor</i> )	Avoid LTU	1.3	1.0	-2.4 <sup>□</sup>	0.04
Milk Snake ( <i>Lampropeltis triangulum</i> )	LTU	-1.3	-1.5	2.8 <sup>□</sup>	0.05
Common Kingsnake ( <i>Lampropeltis getula</i> )	FYB	-1.3	2.5 <sup>□</sup>	-1.3	0.02
Great Plains Rat Snake ( <i>Elaphe emoryi</i> )		-0.7	-0.8	1.5	—
Gopher Snake ( <i>Pituophis catenifer</i> )		1.5	-0.8	-0.7	—

Overall  $\chi^2$  table rejects  $H_0$  for independence of community composition ( $\chi^2 = 158.19$ ,  $df = 20$ ,  $P < 0.001$ ).

□ |2| Possible rejection of independence, ■ |3| Rejection of independence.

AB = Annually burned, FYB = 4-yr burn, LTU = Long-term unburned.

\* Significance testing for each species through Pearson  $\chi^2$ -test for independence.

analyze differences in body size. Individuals residing in long-term unburned areas were significantly larger in SVL (cm;  $F = 3.26$ ,  $df = 46$ ,  $P = 0.047$ ) and mass (g;  $F = 3.81$ ,  $df = 43$ ,  $P = 0.030$ ) than individuals residing in the other burn treatments (Fig. 4).

Four other snake species exhibited only marginal deviance in adjusted residuals  $\geq |2|$  resulting in only marginally insignificant habitat preferences (Table 1). *Tropidoconion lineatum* ( $\chi^2 = 6.0$ ,  $df = 2$ ,  $P = 0.05$ ) preferred annually burned areas, and *L. getula* ( $\chi^2 = 8.0$ ,  $df = 2$ ,  $P = 0.018$ ) preferred an intermediate burn frequency. *Lampropeltis triangulum* ( $\chi^2 = 6.14$ ,  $df = 2$ ,  $P = 0.046$ ) was found in greater number in long-term unburned habitat, whereas *C. constrictor* ( $\chi^2 = 6.33$ ,  $df = 2$ ,  $P = 0.042$ ) was least common there, indicating possible avoidance of unburned habitat.

Species with common habitat or food requirements, responded in similar ways. Overall, amphibian abundances across all detected species indicated a general deficiency in amphibians within the intermediate burn frequency. Although no single species exhibited significant avoidance of this habitat, when summing standard residuals across each of the five species

captured, the total captures were in lower abundances than expected (AB = 7.1, FYB = -6.1, LTU = -0.7). When summed across feeding niches, four small-bodied earthworm eating snakes (*D. punctatus*, *S. dekayi*, *T. lineatum*, and *C. vermis*) were found in much lower abundances than expected in the two higher burn frequencies (AB = -1.4; FYB = -5.1; LTU = 6.8).

## DISCUSSION

This study indicates that different burn treatments in tallgrass prairie do not result in significantly different species richness, evenness, or diversity of reptiles and amphibians. However, community compositions within habitats created by these burn treatments are significantly different from one another. Similarities in species composition followed the burn continuum, with more species shared between more closely related habitats.

This study was designed to discover initial differences of herpetofauna between burn treatments. KPBS watershed design limited the possible areas of study based on size and

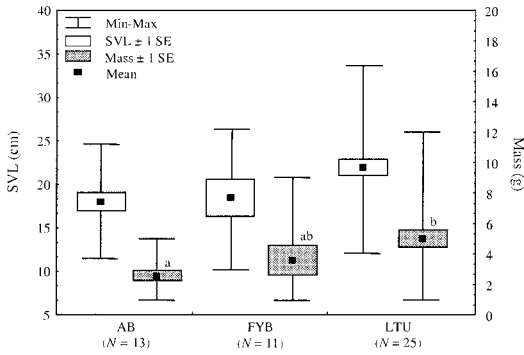


FIG. 4. Body measurements of *Diadophis punctatus* captured in different burn treatments. Significant differences were found between burn frequencies for SVL ( $F = 3.26$ ,  $df = 46$ ,  $P = 0.047$ ) and mass ( $F = 3.81$ ,  $df = 43$ ,  $P = 0.030$ ). Different letters indicate significant pairwise differences. AB = Annually burned, FYB = 4-yr burn, LTU = Long-term unburned.

treatment, leading to insufficient replication. The variability in habitat types within our burn treatment replicates also limits the conclusions of this study. Sufficient replicate sites of the same general size and type are difficult to come by. The 4-yr burn treatments were one year apart in their burn cycle. Observed abundances may depend on species-specific recovery times postburn; thus, patterns within the 4-yr replicates may have been different from each other. Both of the long-term unburned sites were similar in time since fire; however, the habitat types were very different, a 20-yr burn treatment prairie and a gallery forest. The suites of species may be completely different between these sites. Because of the limited replicate possibilities, choice of watersheds was solely based on burn treatment. An increase in transects or watersheds would increase the number of individuals captured within each species, allowing for more treatment comparisons. The small number of individuals captured for each species often limited our conclusions. The trapping protocol used in this study was unable to account for all species found on KPBS, *Spea bombifrons*, *Bufo woodhousii*, *Hyla chrysoscelis*, *Rana catesbeiana*, *Crotaphytus collaris*, *Elaphe obsoleta*, *L. calligaster*, and *Agkistrodon contortrix* are known to be in the area, but no individuals were detected. Biases in diversity indices are possible when all species in an area are not detected. However, we were unable to correct for these biases because of lack of burn regime preferences on all species. The short-term nature of the project may also limit the power of our study to detect significant differences. In this study, sampling was not performed during the summer months (July and August). Because of the intense heat, herpetofaunal activity dramati-

cally decreases and, thus, sampling during this time period is ineffective and can result in increased mortality. Differences in initial sample dates during both seasons were due to different spring burn dates of watersheds used and time constraints. Long-term research may enhance this study and decipher some of the minor difference in species richness and diversity levels.

Fredericksen and Fredericksen (2002) found increased species diversity in tropical forests in postfire habitats. However, the majority of studies in ecosystems similar to tallgrass prairie report confounding results at the community level, with evidence for no change in overall herpetofaunal species diversity (Braithwaite, 1987; Greenberg et al., 1994; Hannah and Smith, 1995) and for decrease in overall herpetofaunal diversity (Mushinsky, 1986; Masters, 1996). Most often, direct responses are evident at the species (Braithwaite, 1987; Fair and Henke, 1997; Woinarski et al., 1999; Cavitt, 2000; Setser and Cavitt, 2003) or niche level (Fyfe, 1980; Greenberg et al., 1994; McLeod and Gates, 1998; Bury, 2004), which confounds results at a community level. Species with positive responses toward the habitat created by a given fire regime will replace those species with negative responses that have emigrated or been extirpated from the area, resulting in an insignificant net change of overall species diversity, such as was found in this study.

Burn regimes can affect species abundances in three ways: (1) direct mortality of individuals caused by fire; (2) alteration of vegetation structure and microhabitat; and (3) alteration in abundance of prey items (earthworms, insects, mammals, birds, and other reptiles) and/or predator abundance. Studies focused on direct mortality on herpetofauna caused by fire have found little impact on the community (Erwin and Stasiak, 1979; Floyd et al., 2001). Mortality rates are likely to be variable between both species and years and based on specific climatic conditions. Air temperature fluctuations also influence body temperature, which directly influences escape speed (Martin and Lopez, 2000; Cooper, 2003). Escape speed and proximity of individuals to shelter could influence probability of direct mortality. Similarly, the loss or change of the vegetation structure in a postburn environment led to increased predation pressures on large snakes by raptors (Wilgers, 2005).

In the few cases in which species specialize on prey types (i.e., earthworm and ant obligates), direct effects on prey abundance may influence the number of species and individuals able to reside in a specific area. The suite of earthworm feeding snakes at KPBS (*D. punctatus*, *S. dekayi*, *T. lineatum*, and *C. vermis*) tended to avoid intermediate and annually burned areas, which may be caused by an increased abundance of

European earthworms within areas of high soil moisture and organic nutrients characteristic of habitats without fire disturbance (Callahan and Blair, 1999). However, most herpetofaunal species found in tallgrass prairie tend to be generalist feeders. Individuals can shift to other prey types when one becomes unavailable, thus, responses of species to different burn regimes may be based on the resulting vegetation structure.

Anurans were found in lower abundances than expected within the intermediate burn frequency. Although there are many intermittent streams running near the transects, no permanent water sources are nearby. Capture of individuals could be caused by movement between major water sources. A few species captured in the study (*Acris crepitans*, *Rana blairi*, and *Pseudacris triseriata*) are known to travel large distances away from water (Collins, 1993). The more extreme and variable microhabitats within annually burned areas could force amphibians to move more frequently to find suitable temperatures and moisture. Thus, it is possible that anuran abundances are similar among burn regimes but that they are more easily detected in annually burned areas caused by increased activity. Low capture numbers limits conclusions drawn from these results and should be taken with caution, future studies on the effects of burning on amphibians are needed.

This study found four species exhibiting significant preferences and/or avoidances of specific burn treatments, whereas five species exhibited preferences that were only marginally insignificant. These trends most often can be explained based on individual species life-history characteristics. Habitats within annually burned areas are typically more spatially variable in vegetation cover, caused by the lack of a litter layer. This leads to a warmer, drier microclimate with an increased number of open basking rocks especially during early spring. Habitat requirements for *E. obsoletus*, and *P. cornutum* (Collins, 1993) suggest that annually burned areas are ideal habitat and our results support this hypothesis. Only one snake species showed clear habitat preferences, whereas four others exhibited marginally insignificant preferences, resulting from a reduction in alpha. *Diadophis punctatus* significantly preferred long-term unburned habitat, which concur with each species' habitat requirements (Collins, 1993). The increased moisture level of soils in long-term unburned areas, along with an abundance of its primary prey, earthworms, makes this an ideal habitat for *D. punctatus*.

*Scincella lateralis* exhibited the most extreme response to any burn frequency across all species. It is the only species showing much larger abundances in the intermediate burn frequency

than would be expected with independent assortment, which was unexpected based on the favored habitat of wooded areas as reported by Collins (1993). The cool-moist habitat created by coverboards, which is more similar to their preferred habitat, may attract individuals within the 4-yr burn treatment. Thus, the capture probability may simply be higher in intermediate burn regime, and abundances are similar between watersheds of lower burn frequencies.

*Coluber constrictor* exhibited a marginally insignificant avoidance of long-term unburned areas; which is not surprising as it is a more open prairie species (Collins, 1993). This finding is contrary to both Cavitt (2000) and Setser and Cavitt (2003) in which *C. constrictor* was found less often in recently burned areas, and in greater numbers in unburned habitats. In newly burned habitats, activity levels should decrease because of limited amounts of cover for the first several weeks postburn. Coverboards provide an ideal detection method for herpetofauna where activity is limited and cover is at a premium. Across the entire study about 61% of captures of *C. constrictor*, including 50% from annually burned areas across the entire study were from coverboards. The lack of coverboards in previous studies (Cavitt, 2000; Setser and Cavitt, 2003) may have resulted in biased sampling through underestimates of this species' abundance.

Annual burning of the Flint Hills region of the tallgrass prairie is widespread. This management plan gives little regard to most of the wildlife inhabiting the region. Instead of the traditional mosaic of burn frequencies across the landscape, much of the area is left devoid of grass and cover more than a few centimeters high until late spring (Robbins et al., 2002). One single large scale burn frequency across an entire managed area eliminates heterogeneity of habitats, decreasing the likelihood of species replacement similar to that of metapopulation dynamics. To maintain herpetofaunal diversity at its highest level, we endorse the recommendations of Fuhlendorf and Engle (2004) and Seig (1997) that the large number of habitats created by a shifting mosaic burn schedule should include a maximum number of species and niche levels.

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APPENDIX 1. Herpetofaunal captures on Konza Prairie Biological Station in different burn frequencies from 2003–2004.

Common name (Scientific name)	Burn frequency									Overall total
	Annual			4-yr			Extended			
	K1B	K1B	(Totals)	K4A	K4B	(Totals)	K20A	AL	(Totals)	
<b>Amphibians</b>										
Northern Cricket Frog ( <i>Acris crepitans</i> )	1	1	(2)	0	0	(0)	0	1	(1)	3
Western Chorus Frog ( <i>Pseudacris triseriata</i> )	0	0	(0)	0	0	(0)	0	1	(1)	1
Plains Leopard Frog ( <i>Rana blairi</i> )	2	0	(2)	0	0	(0)	0	0	(0)	2
American Toad ( <i>Bufo americanus</i> )	1	0	(1)	0	0	(0)	0	0	(0)	1
Great Plains Narrowmouth Toad ( <i>Gastrophryne olivacea</i> )	5	0	(5)	0	0	(0)	0	1	(1)	6
<b>Reptiles</b>										
Ornate Box Turtle ( <i>Terrapene ornata</i> )	6	0	(6)	1	2	(3)	0	1	(1)	10
Ground Skink ( <i>Scincella lateralis</i> )	5	5	(10)	39	33	(72)	2	19	(21)	103
Great Plains Skink ( <i>Eumeces obsoletus</i> )	10	3	(10)	1	1	(2)	0	1	(1)	16
Texas Horned Lizard ( <i>Phrynosoma cornutum</i> )	17	0	(17)	0	0	(0)	0	0	(0)	17
Slender Glass Lizard ( <i>Ophisaurus attenuatus</i> )	2	0	(2)	0	1	(1)	0	4	(4)	7
Ringneck Snake ( <i>Diadophis punctatus</i> )	15	3	(18)	11	6	(17)	16	22	(38)	73
Brown Snake ( <i>Storeria dekayi</i> )	0	0	(0)	1	3	(4)	4	1	(5)	9
Lined Snake ( <i>Tropidoclonion lineatum</i> )	3	0	(3)	0	0	(0)	0	0	(0)	3
Western Worm Snake ( <i>Carphophis vermis</i> )	0	0	(0)	0	0	(0)	0	1	(1)	1
Common Garter Snake ( <i>Thamnophis sirtalis</i> )	0	1	(1)	0	0	(0)	0	4	(4)	5
Eastern Yellow-bellied Racer ( <i>Coluber constrictor</i> )	5	3	(8)	1	8	(9)	1	0	(1)	18
Milk Snake ( <i>Lampropeltis triangulum</i> )	0	2	(2)	0	3	(3)	1	8	(9)	14
Common Kingsnake ( <i>Lampropeltis getula</i> )	0	0	(0)	1	3	(4)	0	0	(0)	4
Great Plains Rat Snake ( <i>Elaphe emoryi</i> )	0	0	(0)	0	0	(0)	0	1	(1)	1
Gopher Snake ( <i>Pituophis catenifer</i> )	0	1	(1)	0	0	(0)	0	0	(0)	1
Total Individuals	72	19	(91)	55	60	(115)	24	65	(89)	294
Total Species	12	8	(15)	7	9	(9)	5	13	(14)	20