



ELSEVIER

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*)

Daniel Steven Harvey*, Patrick J Weatherhead

Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 606 East Healey Street, Champaign, IL 61820-5502, United States

ARTICLE INFO

Article history:

Received 24 February 2005

Received in revised form

13 December 2005

Accepted 20 December 2005

Available online 10 February 2006

Keywords:

Sistrurus catenatus catenatus

Bruce Peninsula, Ontario

Hierarchical habitat selection

Microhabitat selection

Edge habitat

ABSTRACT

Understanding the process animals follow to select habitat, rather than just documenting the habitat they use, will improve our ability to predict how the animals use habitat in other locations and how they will respond to changes in habitat. Animals are usually assumed to select habitats hierarchically, preferentially using specific macrohabitats at a landscape scale and specific microhabitats within the preferred macrohabitats. We used four years of telemetry data from 34 individuals to test this hierarchical model of habitat selection with eastern massasauga rattlesnakes (*Sistrurus c. catenatus*) in Ontario. Snakes were selective at the microhabitat scale, preferentially using locations with closer retreat sites and shrubs than random. Gravid females were most selective, using sites with more rock cover and less canopy closure than sites used by males and nongravid females. Snakes preferred forested habitats for hibernation and steadily increased their use of open, wetland, and edge habitats to a peak in mid-summer. Landscape-scale habitat preferences were generally mild and could be explained by the relative availability of suitable microhabitat within habitats, suggesting habitat selection was primarily driven by microhabitat preferences. The lack of selectivity at the landscape scale may be a consequence of fine-grained differences between habitats that allow massasauga rattlesnakes to find suitable microhabitats in all available macrohabitats. For species that select habitat primarily at the microhabitat scale (e.g., the rattlesnakes we studied), landscape-scale modeling of habitat use will only be effective to the extent habitats reflect the availability of suitable microhabitat within.

© 2006 Elsevier Ltd. All rights reserved.

1. Introduction

The preeminent importance of habitat loss to declining biodiversity (Meffe and Carroll, 1997; Wilcove et al., 1998) makes identification and protection of critical habitat a primary goal of most conservation programs. Identifying habitats that are used selectively is the first step in determining a species' critical habitat. Habitat selection can occur at different spatial scales. At the landscape scale, animals can select

the most suitable habitats (i.e., forest, field, wetland) and then within habitats, animals can select microhabitats that best meet their needs (Cody, 1985; Orians and Wittenberger, 1991). Our general goal in this study was to determine whether eastern massasauga rattlesnakes (*Sistrurus c. catenatus*) follow such a hierarchical approach to habitat selection, and to identify both the habitats and microhabitats used most in proportion to their availability. Habitat at both scales was characterized structurally, because snakes often

* Corresponding author: Tel.: +1 217 898 4080/333 2235; fax: +1 217 265 0056.

E-mail address: harvey_da@yahoo.ca (D.S. Harvey).

0006-3207/\$ - see front matter © 2006 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.12.015

use structural cues to recognize superior habitat for thermoregulation, avoiding predators, and capturing prey (Mullin and Gutzke, 1999; Theodoratus and Chiszar, 2000; Tsairi and Bouskila, 2004).

Apparent hierarchical selection (disproportionate use of habitat relative to availability at multiple spatial scales) could arise in two ways. The pattern could be true hierarchical habitat selection, as described above. Alternatively, snakes could select only microhabitat, using macrohabitats in proportion to the availability of suitable microhabitat within each of them. Apparent landscape-scale preferences could then simply be an artifact of suitable microhabitats being limited to preferred habitats (Allen and Starr, 1982; O'Neill et al., 1986; Kotliar and Wiens, 1990). Discounting the latter possibility requires demonstration of preference for a particular macrohabitat exceeding what is expected based on microhabitat availability (Wiens, 1989). Numerous studies of birds and mammals have found habitat selection patterns that could not be explained in terms of selection at finer scales (Gutzwiller and Anderson, 1987; Bergin, 1992; Rettie and Messier, 2000; Rolstad et al., 2000; Cushman and McGarigal, 2002; McLoughlin et al., 2002; Grand and Cushman, 2003; McLoughlin et al., 2004). Rubio and Carrascal (1994) proposed that ectotherms may be less likely to select habitat hierarchically than birds and mammals, because the need to thermoregulate behaviorally would increase their dependence on local conditions when selecting habitat. Selectivity at multiple spatial scales has been observed in snakes (Reinert, 1993; Shine and Fitzgerald, 1996; Blouin-Demers and Weatherhead, 2001a; Heard et al., 2004), but these studies did not explicitly test whether broad-scale patterns might be a reflection of finer-scale processes. Our goal was to determine whether landscape-scale preferences by massasauga rattlesnakes could be explained by the availability of microhabitat within habitats.

Both geographic location and foraging mode can affect the importance of habitat selection for snakes, and both should make habitat selection important for the rattlesnake population we studied. Because snakes regulate body temperature behaviorally, selection of thermally appropriate habitat is particularly important for populations in cooler climates (e.g., Blouin-Demers and Weatherhead, 2001a,b). The population we studied was near the northern limit of massasauga rattlesnake distribution. For species such as rattlesnakes that hunt by ambushing prey, habitat selected in which to wait for prey must satisfy multiple needs (feeding, thermoregulation, predator avoidance) for longer periods of time than locations used by species that are active hunters, further increasing the importance of habitat selection. In addition to these ecological considerations, habitat loss is thought to be the primary cause of the disappearance of massasauga rattlesnakes from 40% of counties with historical records of their presence (Symanski, 1998), making understanding how these snakes select habitat important to their conservation.

Eastern massasauga rattlesnakes have been described as occurring in wetlands and grasslands (Wright, 1941; Reinert and Kodrich, 1982; Seigel, 1986; Weatherhead and Prior, 1992; Johnson, 2000), with some use of forests (Seigel, 1986; Weatherhead and Prior, 1992). Most of these studies

described habitat use patterns qualitatively and did not determine whether certain habitats were used disproportionately. Weatherhead and Prior (1992) compared habitat use relative to availability for massasauga rattlesnakes on the Bruce Peninsula, Ontario, combining GIS and radio telemetry data. While methodologically a step forward, their study was limited by having tracked only a small number of snakes ($n = 11$), most of which were males. Female snakes of certain species select habitat that differs from that selected by males, particularly when females are gravid (see Reinert, 1993 for a review). Microhabitat selection by massasauga rattlesnakes is even less well studied than landscape-scale habitat selection, limited to associations of snakes with local vegetation (Wright, 1941; Reinert and Kodrich, 1982).

In determining patterns of habitat selection by massasauga rattlesnakes, we were particularly interested in edge habitat at the landscape scale. Blouin-Demers and Weatherhead (2001a,b) showed that black ratsnakes (*Elaphe obsoleta*) in a northern population preferentially used edges between forested and open habitats, particularly when their need to thermoregulate was high. The massasauga rattlesnakes we studied were also near the northern limit of their range, thus edge habitat could be important for thermoregulation. Because thermoregulatory demands are likely to vary seasonally and by reproductive condition (e.g., Blouin-Demers and Weatherhead, 2001a), we determined whether habitat selection varied by month of the active season, or by sex and reproductive condition (males, nongravid females, gravid females). We analyzed habitat used for hibernation separately from the active season. The snakes' habitat needs while hibernating seem likely to be determined by features below ground, and these may differ from, or not be predicted by, above-ground habitat used by snakes while active (e.g., Prior and Weatherhead, 1996).

2. Methods

2.1. Study site

We conducted our research from 2001 to 2004 on the Upper Bruce Peninsula (50°04'N, 45°44'W), Ontario, Canada, approximately 50 km from the northern limit of the species' distribution. To include all major (>1% of the total area) habitats in this area, we used two study sites 12.5 km apart. Singing Sands site borders Lake Huron and consists of a mix of sand dunes, alvars, wetlands, deciduous forest, and coniferous forest, plus a parking lot, beach, and hiking trail. Warder Ranch has a mixture of wetlands, deciduous forest, coniferous forest, and a large successional field on which grazing ended about 25 years ago.

2.2. Radio telemetry

We initially found rattlesnakes opportunistically by searching all habitats at both study sites. A concurrent study confirmed the likelihood of detecting a snake by systematic searching was similar in all habitats (Harvey, 2005). Most subsequent captures resulted from finding new snakes associated with snakes we were tracking. We sexed snakes using cloacal

probes and the reproductive condition of females was based on whether or not they gave birth that season. A snake was considered shedding if we observed it shedding, if we found the snake near a shed skin, or when the cloudy appearance of its eyes indicated shedding was imminent.

We implanted snakes with 11 g transmitters in 2001 and 2002 and 9 g transmitters in 2003 (Model SI-2T, Holohil Systems Inc., Ontario). Surgical procedures generally followed Reinert and Cundall (1982). Post-surgery, snakes were held for three days and then released at the point of capture. In total, 19 males, 9 gravid females, and 6 nongravid females were implanted with transmitters. Five females were gravid in one year and nongravid the next year, and one female went from nongravid to gravid between years.

We used radio telemetry to relocate snakes on average every two days until they entered hibernation and again when they re-emerged the following spring. Exact positions were recorded in Universal Transverse Mercator (UTM) coordinates (North American Datum of 1983) using a handheld global positioning system unit (GPS 12XL) with a mean precision of 4.6 m. On 2 separate occasions we tracked snakes for 48 continuous hours (at 3 h intervals), revealing snakes did not move at night. We considered a snake to have used different hibernation sites in different years if the sites were >20 m apart.

2.3. Landscape-scale habitat characterization

We characterized the habitats in our study sites using Landsat TM 7 satellite images taken in 1999. Environmental Analysis and Scientific Interface/Picture Analysis, Correction, and Enhancement (EASI/PACE) software was used to process the images. Of the 17 habitat classifications on the Upper Bruce Peninsula, 12 occurred in our study sites (Table 1). These 12 categories collectively account for >99% of the land area of the Upper Bruce Peninsula. A separate study in the area determined the habitat classifications were highly accurate (>85%) with the exception of dense mixed forests being commonly confused with dense coniferous forests (Coady, 2005).

Following Blouin-Demers and Weatherhead (2001a), we defined edge habitat as the area within a specified distance of a forested/nonforested habitat interface. Without knowing how far from a habitat interface massasauga rattlesnakes perceive as edge, we compared use and availability of edge habitat using distances from 5 to 30 m (in 5 m increments) from an interface to characterize edge. Given preferential use of edges, the distance at which the snakes perceive edges should yield the greatest use of edge relative to its availability. By using this distance, we avoided defining edge subjectively.

We used the area within a 240 m buffer around the positional locations recorded for each snake (minus overlap) to delimit the habitat available to that snake (240 m was the upper 95% quantile of the two-day movement distance by males and nongravid females). Locations were pooled for individual snakes tracked in multiple years, except for females whose reproductive status changed between years. For each snake we calculated the proportions of each habitat type within the area defined as 'available' using ArcGIS, excluding open water because massasauga rattlesnakes are terrestrial.

Table 1 – Mean (\pm SE) percentages of habitat used by and available to eastern massasauga rattlesnakes ($n = 40$) in the study areas from 2001 to 2004 and the regional habitat composition on the Upper Bruce Peninsula, Ontario

Habitat	% Use	% Available	% Upper Bruce Peninsula
<i>Open</i>			
Pasture, abandoned field	22.5 \pm 4.2	14.6 \pm 2.7	5.9
Cropland	6.7 \pm 2.0	2.8 \pm 0.7	9.5
Bedrock outcrop, exposed sand, alvar	5.6 \pm 2.6	3.9 \pm 1.1	2.0
<i>Wetland</i>			
Open bog	3.2 \pm 0.9	4.5 \pm 0.5	1.3
Treed bog	3.8 \pm 1.7	3.1 \pm 0.5	3.1
Coniferous swamp	1.0 \pm 0.2	2.4 \pm 0.3	1.5
Marsh	0.1 \pm 0.1	1.6 \pm 1.4	1.1
Deciduous swamp	0.1 \pm 0.1	0.1 \pm 0.0	0.5
<i>Sparse forest</i>			
Sparse forest	24.2 \pm 4.1	18.8 \pm 1.7	10.5
<i>Dense coniferous forest</i>			
Dense mixed forest	9.1 \pm 3.0	11.0 \pm 1.8	23.1
Dense coniferous forest	7.3 \pm 3.0	5.7 \pm 1.1	14.4
<i>Dense deciduous forest</i>			
Dense deciduous forest	16.5 \pm 2.9	31.6 \pm 3.2	27.1
See text for details on the delineation of available habitat.			

2.4. Microhabitat characterization

We quantified microhabitats approximately once per week per snake, within 2–3 weeks of the snake vacating a site. Assessments were conducted only from mid-May to late September to avoid disrupting hibernation behavior. No individual snake represented >7% of microhabitat observations. We used 14 plotless and plotted structural variables (Table 2) derived from previous studies (Reinert, 1984; Prior and Weatherhead, 1996; Blouin-Demers and Weatherhead, 2001a) to quantify microhabitat. Following those studies, plots were centered on the position the snake had occupied, and sampling radii varied from 0 to 30 m depending on the feature being measured (Table 2). 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). To quantify the microhabitat available to the snakes, we conducted identical assessments at locations selected randomly near where snakes were observed. In 2002, each location was a randomly generated distance (0–84 m) and direction from each snake-selected site, where 84 m was the upper 95% confidence interval of mean daily movement rate from a previous study on the Bruce Peninsula (Weatherhead and Prior, 1992). We expanded that limit to 240 m in 2003 to reflect the more extensive movements we documented in this study. We combined random samples from both seasons because locations sampled in 2002 (20% of the total) fell largely in the area sampled in 2003. We used the same sampling scheme for gravid

Table 2 – Structural habitat variables used in the analysis of microhabitat selection by eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, in 2002 and 2003

Variable	Definition	Radius ^a (m)
DOS	Distance (m) to nearest overstory tree (>2 m tall, >7.5 dbh ^b)	30
DUS	Distance (m) to nearest understory tree (>2 m tall, <7.5 dbh)	30
DSHRUB	Distance (m) to nearest shrub (<2 m tall)	30
DROCK	Distance (m) to nearest rock (>20 cm maximum length)	30
DLOG	Distance (m) to nearest log (>7.5 cm maximum diameter)	30
DRETREAT	Distance (m) to nearest retreat site ^c	30
HSHRUB	Height (cm) of the nearest shrub	30
%ROCK	Coverage of rocks (%) within plot	1
%LOG	Coverage of logs (%) within plot	1
%LEAF	Coverage of leaf litter (%) within plot	1
%VEG	Coverage of vegetation (i.e., shrubs, grasses) (%) within plot	1
%WATER	Coverage of water (%) within plot	1
#WSTEM	Total number of woody stems within plot	1
%CANCOV	Canopy cover (%) above plot	0

a Maximum distance from the center of the plot the variable was measured.

b Diameter at breast height.

c A retreat site was the nearest location a snake could avoid capture.

females because they occasionally move as far as males and non gravid females, despite moving less often.

2.5. Data analyses

Statistical analyses were performed using a combination of Excel 2002, JMP 4.0.0, SPSS Version 13.0, Systat Standard Version 11, ArcView GIS 3.3 and ArcGIS 8.3. Means are reported ± 1 SE.

2.5.1. Landscape-scale analyses

Habitat preferences on a landscape scale were determined using compositional analysis (Aebischer et al., 1993). A habitat composition represents the proportion of time spent in each habitat type. A single composition was created for each snake, combining data from all years for individuals tracked in multiple years. For females whose reproductive status changed between years, we computed separate compositions each year. We removed habitats representing <3% of a snake's composition because rare habitats can have a disproportionate effect on compositional analysis. We added 0.01 to all use and availability proportions prior to analyses to avoid undefined log-ratios. Compositional analysis was performed with all observations and then repeated with observations categorized by sex and reproductive condition and by study site. From all shedding observations we created a single habitat composition, containing the proportion of shedding observations in each habitat type. This shedding composition was compared with the "available" habitat compositions of each snake to determine if habitat used for shedding differed

from that generally available to snakes. We repeated this procedure using hibernation sites and courting/mating sites in place of shedding sites.

2.5.2. Microhabitat analyses

We used multivariate analysis of variance (MANOVA) to test whether the microhabitat of snake-selected and random locations differed. We used discriminant function analysis (DFA) to interpret group differences. Analyses were repeated with observations divided by month for seasonal analysis.

In cases where a structural feature did not occur within the prescribed sampling radius (55 of 8624 measured variables, 0.6%), the mean value for the variable category was substituted for the missing value. We removed one variable from pairs of highly correlated ($|r| > 0.7$) variables from analyses to reduce multicollinearity. A combination of arcsine, log-normal, and square root transformations improved the fit of each remaining variable to a normal distribution (Shapiro-Wilk tests, mean $W = 0.80$). We conducted Box's M test prior to all multivariate tests and in all cases the covariance matrices were found to be heterogeneous ($p < 0.001$). This is expected with ecological data and previous authors have defended the heuristic value of multivariate tests despite deviation from this assumption (Reinert, 1984; Blouin-Demers and Weatherhead, 2001a).

2.5.3. Testing for hierarchical habitat selection

We tested for hierarchical habitat selection using the probable finest (microhabitat) and coarsest (landscape) scales of selection during a snake's active season. Locally, the topography of the Bruce Peninsula is uniform (generally flat) relative to the diversity of vegetation (Bennet, 1992). Thus, we assumed most of the structural variation relevant to massasauga rattlesnakes was captured by our habitat classifications at the landscape scale. As with any habitat selection study, it is possible snakes selected habitat on scales or according to factors that were not considered. Because there is little evidence to the contrary in snakes, we assumed habitat selection was density-independent (but see Webb and Shine, 1997).

To determine the relative availability of suitable microhabitat within habitats, we conducted DFA comparing random and snake-selected locations. We then used the classification feature in DFA to determine the percentage of random sites "incorrectly" classified as snake-selected sites in each habitat, and assumed this reflected the relative percentage of microhabitat suitable for snakes within each habitat. We conducted compositional analysis with habitat availability weighted by the availability of suitable microhabitat within habitats to determine whether landscape-scale preferences could be explained by selection of microhabitats. Hierarchical selection would be indicated if preferences remained after macrohabitats were weighted by their availability of suitable microhabitats.

3. Results

We recorded 2546 locations from 34 individual rattlesnakes over the course of the study. The number of observations per snake varied from 15 (1 month) to 168 (14 months over 3

years), with a mean of 75 (5 months, roughly one full field season). Predators killed at least six snakes during the study. We sampled microhabitat at 308 of 2546 snake locations and at 308 random sites.

3.1. Landscape-scale habitat selection

Because many habitat types were rare and seldom used, we condensed the 12 habitat categories into 5 (Table 1). Dense mixed forest was considered collectively with dense coniferous forest because the former contained primarily coniferous trees (Coady, 2005). Our sixth landscape category, “edge”, was defined as the interface between any forested and nonforested (i.e., open, wetland) habitat. Using distances from 5 to 30 m (in 5 m increments) from an interface to characterize edge, we found the difference between edge use and availability increased from 1% at 5 m to a peak of 27% at both 15 and 20 m, and then declined to 18% at 30 m, suggesting massasauga rattlesnakes perceive edge at a distance of approximately 15–20 m. Because other snakes are known to use habitat selectively within 15 m of a forest edge (Blouin-Deemers and Weatherhead, 2001a), we used 15 m to categorize edge in subsequent analyses.

Habitat preferences on a landscape scale were generally mild. Overall, snakes used dense deciduous forest slightly less than expected relative to availability and all other habitats slightly more (Table 3). No habitat represented <10% or >25% of overall habitat use. Contrary to our prediction, gravid females were not strongly selective in their use of habitat (Table 3). We observed males and females within 1 m of each other on 39 occasions in July and August. Because same-sex pairs were rare, as were pairs observed early or late in the season, we equated proximity with courting or mating (two observations did involve copulation). Snakes used habitat

selectively for courting/mating, but preferences were similar to those of all snakes (Table 3).

Habitat use varied seasonally. Snakes preferred forested habitats (dense deciduous, dense coniferous, and sparse forest) for hibernation (Table 3), and used forested habitats almost exclusively in the months immediately prior to and following hibernation (Fig. 1). Use of open, wetland, and edge habitat increased from hibernation to a peak in mid-summer (Fig. 1). Habitat use during the summer was variable, with snakes most heavily using open habitat (Fig. 1). When snakes were shedding they preferred open and wetland habitat (Table 3). However, this trend could be coincident with the more extensive use of open and wetland habitat during the summer, because most shedding occurred in late June or early July (18 of 24 observations, 75%).

3.2. Microhabitat selection

The variables %LEAF, #WSTEM, and DOS were highly correlated with other variables (%VEG $r = -0.81$, DSHRUB $r = -0.75$, and %CANCOV $r = -0.75$, respectively) and thus were removed from analyses. Microhabitat used by males, nongravid females, gravid females, and random locations differed ($A = 0.65$, $F_{433,1753} = 8.33$, $p < 0.001$), with all groups different from one another ($F_{11,595} > 2.50$, $p < 0.004$). Interpreting the first two discriminant functions (which accounted for >90% of the variation among groups), gravid females used locations with more nearby rock cover, closer retreat sites, and less canopy cover than the other groups (Fig. 2). Males and nongravid females used sites with closer retreat sites and less rock cover than random (Fig. 2). Gravid females were slightly closer, on average, to retreat sites than were other snakes (0.4 vs. 0.5 m). The gravid female centroid was furthest from the centroid for random samples in discriminant space (Fig. 2),

Table 3 – Habitat use, availability, and preference by eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, from 2001 to 2004 as determined by compositional analysis

Category	N	% Use/% available						Avoided↔Preferred	Statistics		
		Open (OP)	Wetland (WE)	Edge (ED)	Sparse forest (SP)	Dense coniferous forest (DC)	Dense deciduous forest (DD)		λ^a	F	p
All snakes	40	23.1/16.3	10.5/9.0	13.7/10.8	17.5/14.8	20.3/19.7	14.9/29.3	DD <u>WE</u> ED SP DC OP	0.67	3.41	0.013
By behavior ^b											
Shedding	40	41.7/16.3	29.2/9.0	4.2/10.8	16.7/14.8	8.3/19.7	0.0/29.3	DD ED <u>DC</u> <u>SP</u> <u>WE</u> OP	0.02	327.18	<0.001
Courting/Mating	40	27.0/16.3	10.8/9.0	21.6/10.8	13.5/14.8	8.1/19.7	18.9/29.3	<u>DC</u> <u>DD</u> <u>SP</u> <u>WE</u> ED OP	0.33	14.57	<0.001
Hibernation	40	0.0/16.3	0.0/9.0	7.7/10.8	25.6/14.8	30.8/19.7	35.9/29.3	<u>OP</u> <u>WE</u> ED <u>DD</u> <u>SP</u> <u>DC</u>	0.09	67.79	<0.001
By sex and condition ^c											
Males	19	26.3/16.6	12.6/9.6	11.9/10.6	13.3/12.0	22.2/24.0	13.6/27.1	DD <u>SP</u> <u>DC</u> ED WE OP	0.57	2.16	0.118
Nongravid females	11	18.7/15.7	13.4/7.7	17.1/10.3	20.9/18.4	7.2/11.0	22.7/36.9	<u>DD</u> <u>DC</u> <u>OP</u> <u>SP</u> <u>ED</u> <u>WE</u>	0.59	0.85	0.563
Gravid females	10	21.9/16.5	3.1/9.4	13.4/11.7	21.9/16.2	31.1/21.1	8.7/25.1	<u>WE</u> <u>DD</u> <u>ED</u> <u>DC</u> <u>SP</u> <u>OP</u>	0.18	4.62	0.059
By study site											
Singing Sands	20	5.3/6.8	8.7/6.2	18.2/9.5	28.7/22.9	10.9/8.6	28.2/46.1	<u>DD</u> <u>OP</u> <u>WE</u> <u>DC</u> <u>SP</u> <u>ED</u>	0.58	2.16	0.114
Warder Ranch	20	40.9/25.9	12.2/11.9	9.3/12.1	6.4/6.8	29.7/30.8	1.6/12.5	DD <u>ED</u> <u>WE</u> <u>SP</u> <u>DC</u> OP	0.25	9.80	<0.001

See text for details on the delineation of available habitat. Habitats that share a common underline were equally preferred.

a Wilk's lambda.

b Percentage use was determined using 24 shedding, 37 courting/mating, and 39 hibernation observations.

c Reproductive condition.

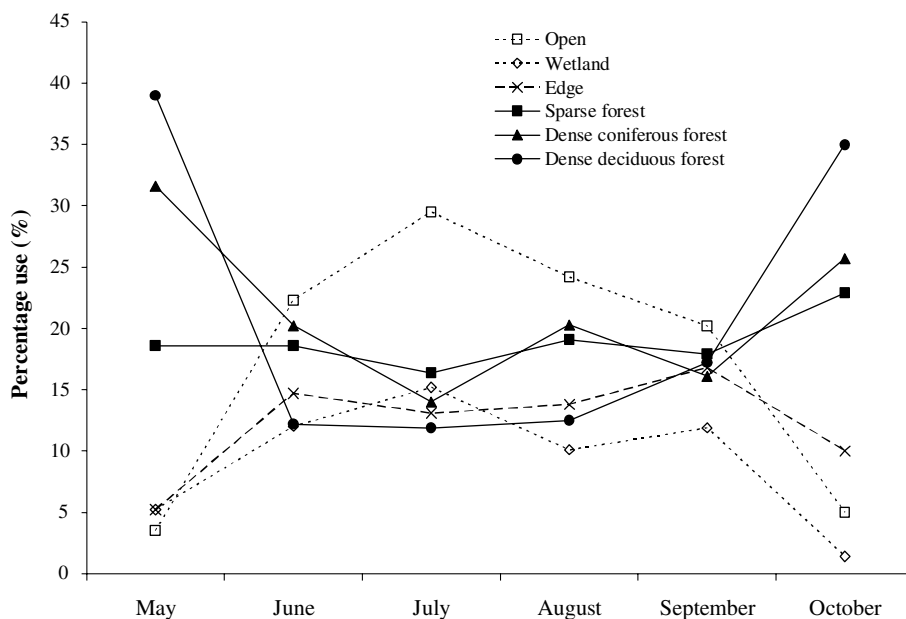


Fig. 1 – Seasonal pattern of habitat use by eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, from 2001 to 2004.

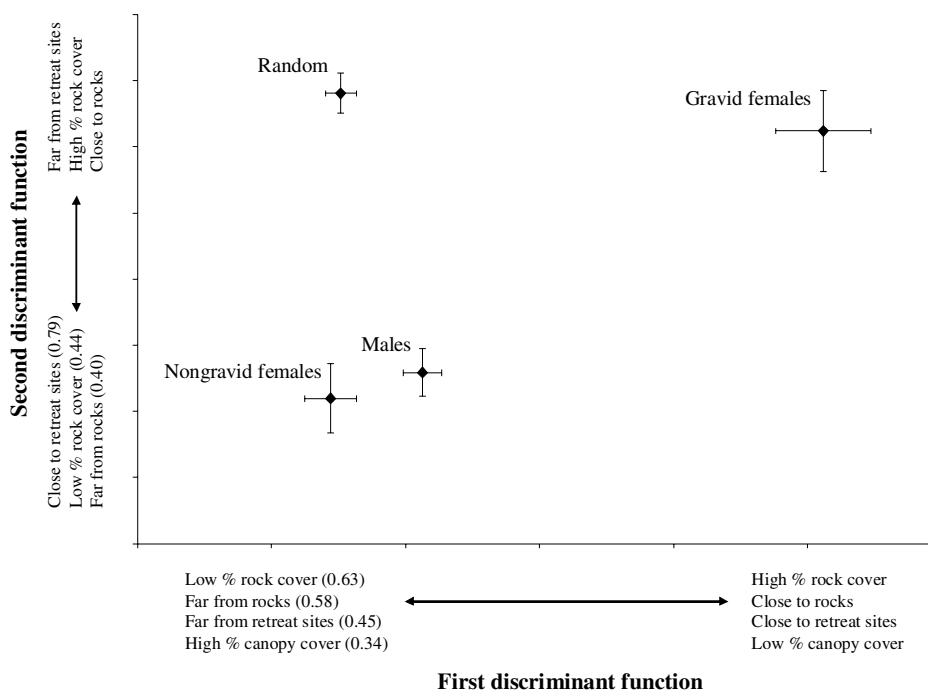


Fig. 2 – Mean (\pm SE) discriminant function scores of gravid female, nongravid female, male, and random microhabitat for eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, in 2002 and 2003. Variables with structural coefficients >0.3 are shown (structural coefficients in parentheses).

suggesting that gravid females were the most selective with regard to microhabitat.

Microhabitat use varied seasonally ($\lambda = 0.77$, $F_{44,1122} = 1.81$, $p = 0.001$). DFA with observations divided by month produced a function describing a gradient based primarily on proximity to woody features (i.e., leaf litter cover, overstory trees, understory trees, logs, shrubs; each other function explained

$<30\%$ of variation among months). Snakes were nearest to woody features after emerging from hibernation in the spring and furthest from those features in the middle of summer (Fig. 3).

The microhabitats of snake-selected and random locations at Singing Sands and Warder Ranch were different ($\lambda = 0.80$, $F_{33,1774} = 4.26$, $p < 0.001$). Differences between snake-selected

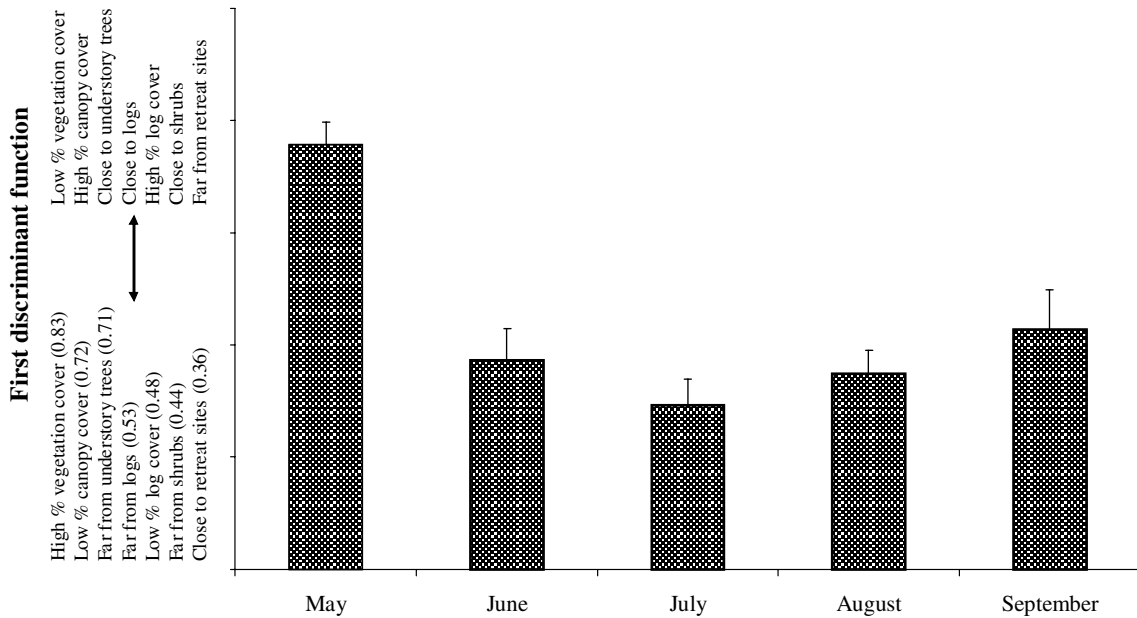


Fig. 3 – Mean (±SE) discriminant function scores of snake-selected microhabitat by month for eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, in 2002 and 2003. Variables with structural coefficients >0.3 are shown (structural coefficients in parentheses).

and random locations within sites ($F_{11,602} > 4.73, p < 0.001$) exceeded differences in microhabitat use between sites ($F_{11,602} = 1.66, p = 0.078$). The first discriminant function (accounting for 82% of the variation in microhabitat between groups) separated snake-selected and random microhabitat regardless of whether locations were from Singing Sands or Warder Ranch (Fig. 4). Snakes used locations with closer re-

treat sites and shrubs than random at both study sites (Fig. 4).

The most consistently preferred microhabitat feature among snakes was a nearby retreat site (Figs. 2–4). Snakes were closer to retreat sites in every habitat (t-tests, Bonferroni $p = 0.008, p < 0.005$), suggesting snakes selected habitat similarly in all habitats. The habitats with the most random

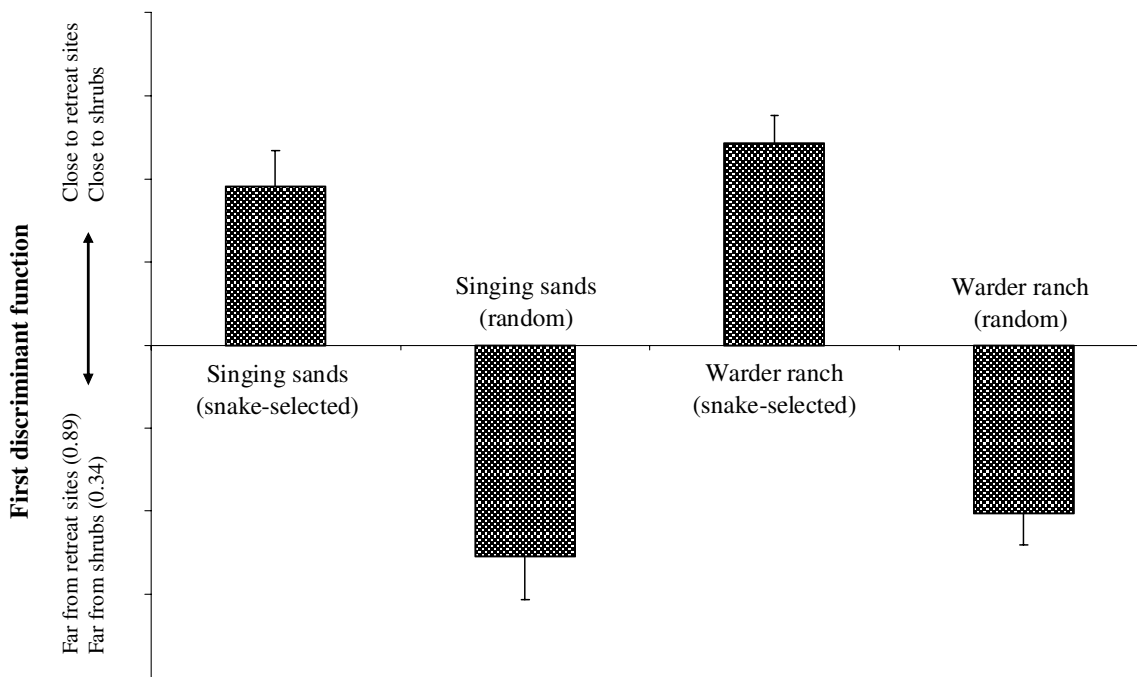


Fig. 4 – Mean (±SE) discriminant function scores of snake-selected and random microhabitat by study site for eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, in 2002 and 2003. Variables with structural coefficients >0.3 are shown (structural coefficients in parentheses).

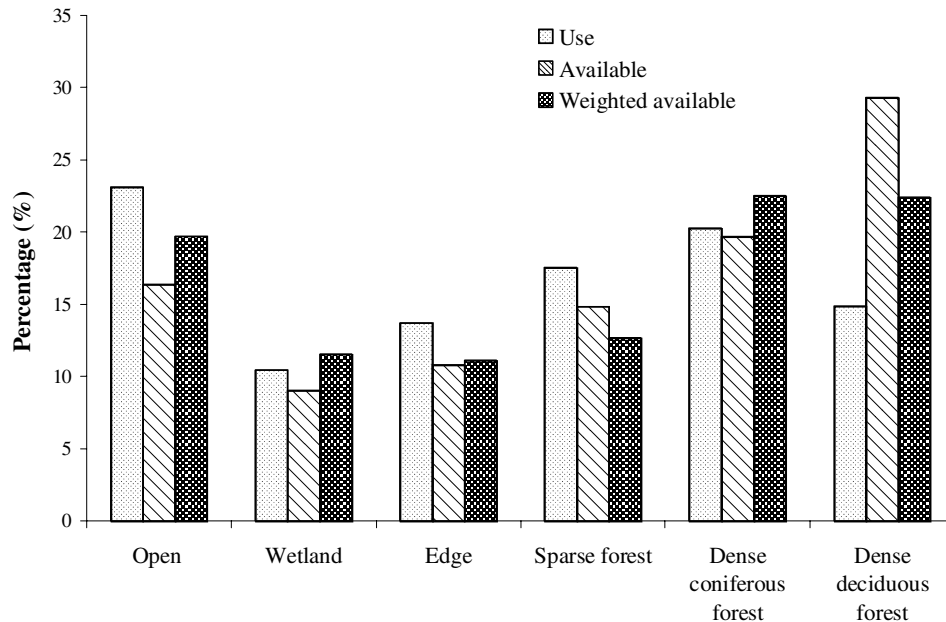


Fig. 5 – Habitat use, availability, and availability weighted by microhabitat availability within habitats for eastern massasauga rattlesnakes on the Upper Bruce Peninsula, Ontario, from 2001 to 2004.

locations that structurally were more similar to snake-selected than random microhabitat (i.e., misclassified by DFA as snake sites) were open and wetland (44% each), followed by dense coniferous forest (41%), edge (35%), sparse forest (26%), and dense deciduous forest (23%). We repeated the overall compositional analysis with habitats weighted by the respective availability of suitable microhabitat within each. This analysis reduced the trend toward habitat preferences relative to the unweighted analysis ($t = 0.77$, $F_{5,35} = 2.10$, $p = 0.089$), in particular explaining the disproportionate use of the most (open) and least (dense deciduous forest) preferred habitats (Fig. 5). Thus, snakes used habitats roughly in proportion to the availability of suitable microhabitat.

4. Discussion

We did not detect evidence of hierarchical habitat selection by eastern massasauga rattlesnakes. Landscape-scale habitat preferences were generally mild and could be explained by the relative availability of suitable microhabitat within habitats. At the microhabitat scale, snakes selected locations with closer retreat sites and shrubs than random, although habitat selection varied by reproductive condition and month. Before considering broader implications of our results for the hierarchical model and for massasauga rattlesnake conservation, we consider the ecology of massasauga rattlesnake habitat selection.

4.1. Massasauga rattlesnake habitat selection

Eastern massasauga rattlesnakes on the Upper Bruce Peninsula could best be described as habitat generalists. Snakes made broad use of available habitats (Table 1) and few features differentiated snake-selected from random locations at the microhabitat scale. These habitat preferences are

weaker than those reported in a previous study of the same massasauga rattlesnake population (Weatherhead and Prior, 1992). The difference could be attributed to the larger sampling effort in our study (more snakes over a larger area for a longer time) that resulted in documentation of extensive habitat use in areas considered “avoided” in the previous study (e.g., grasslands).

Snakes remained close (within ~0.5 m) to retreat sites at all times, likely in an effort to reduce predation risk (nearly one-fifth of snakes with transmitters were depredated). The most common anti-predator behaviors in rattlesnakes are crypsis and flight (Klauber, 1982; Greene, 1988; Prior and Weatherhead, 1994), with flight more likely to be successful if retreat sites are nearby (Greene, 1988). Because snakes were not closer to retreat sites in areas with more human activity in our study or in a previous massasauga rattlesnake study (Parent and Weatherhead, 2000), association with retreat sites was unlikely a response to our presence. Retreat sites might also provide thermal advantages (Huey et al., 1989; Webb and Shine, 1998; Kearney, 2002). Snakes tended to use locations with nearby shrubs. This type of ground cover may help conceal the snake from potential prey (Tsairi and Bouskila, 2004) and provide protection from predators (Charland and Gregory, 1995; Theodoratus and Chiszar, 2000). Perhaps surprisingly for an ectotherm near the northern limit of its range, only gravid females selected locations with a lower percentage of canopy cover than random. This may reflect the generally low canopy coverage at our study sites (mean 25% canopy cover at randomly sampled microhabitat) rather than an indifference towards exposure to incident radiation (which would only be accessible in areas without complete canopy closure).

Gravid females selected sites that were rockier and had less canopy closure than sites selected by males and non-gravid females. Similar habitat preferences have been observed

in gravid *Crotalus horridus* (Reinert, 1984) and gravid *Crotalus viridis* (Graves and Duvall, 1993). These features may allow for warmer or less variable body temperatures during embryonic development (Huey et al., 1989; Reinert, 1993; Lourdaïs et al., 2004), in turn leading to reduced gestation times or improved offspring quality (Shine, 1995). Gravid females selected a more specialized set of microhabitat features than males or nongravid females, but that did not result in gestation sites being concentrated in only a few habitat types. A beaver lodge in a marsh, a large, flat rock in a field, a juniper on an alvar, and the edge of a gravel path in a forest were all used for gestation.

Snakes exhibited a seasonal habitat use pattern, with habitat at or near hibernation sites differing from that selected throughout the rest of the season. Snakes hibernated singly in forested areas, often in the root systems of trees or in rock crevices. Snakes continued to use forested habitats throughout the active season, but increased their proportional use of open, wetland, and edge habitat to a peak in mid-summer. Seasonal habitat use patterns have been observed in multiple massasauga rattlesnake populations (Reinert and Kodrich, 1982; Seigel, 1986; Johnson, 2000), and are presumably driven by the inability of a single area to meet all of a snake's requirements throughout the season (Johnson, 2000).

The importance of edge habitat was ambiguous. At Singing Sands edges were preferred, whereas at Warder Ranch edge was used less than expected given availability. Edges may have been of greater importance at Singing Sands because they provided exposure to open habitat which was less available at Singing Sands than at Warder Ranch. Edge habitat may be of greater importance for thermoregulation in northern snake populations with extensive use of continuous forests, where thermoregulatory options are more limited (e.g., black ratsnakes, Blouin-Demers and Weatherhead, 2001a,b).

4.2. Implications for the hierarchical model of habitat selection

While much has been learned about the ultimate factors guiding habitat selection in snakes (e.g., Blouin-Demers and Weatherhead, 2001b; Shine and Sun, 2002; Pringle et al., 2003; Clark, 2004), less is known about the decision-making process snakes follow to evaluate and select from the different habitats available to them. Reinert (1993) proposed that snakes select habitat hierarchically. Snakes in our study used both microhabitat and macrohabitat selectively, as predicted by the hierarchical model. However, landscape-scale habitat preferences were generally mild and could be explained by the relative availability of suitable microhabitat within habitats, suggesting habitat selection was primarily driven by microhabitat preferences. Snakes may use relevant environmental gradients and/or chemical, climate, and visual cues to detect and evaluate suitable microhabitat, with general search patterns and specific site selection influenced by previous experience (see Ford and Burghardt, 1993; Reinert, 1993 for reviews).

Our failure to detect hierarchical habitat selection does not necessarily indicate that snakes did not select habitat hierarchically. Snakes could be selective at the landscape scale, with habitat preferences directly proportional to (and

perhaps evolving from) the availability of suitable microhabitat within habitats. Testing for this possibility would require manipulation of the availability of suitable microhabitat within habitats, to determine whether habitat preferences are fixed or vary with the amount of suitable microhabitat available.

In the one previous study testing hierarchical habitat selection in reptiles, Rubio and Carrascal (1994) found the habitat features selected by the Spanish lizard *Algyroides marchi* were highly consistent across three spatial scales. The features preferred by lizards (e.g., large rocks, northern aspect, places with water) seemed likely to relate to temperature and humidity, leading them to speculate that ectotherms may be less likely than endotherms to select habitat hierarchically because physiological needs will increase their dependence on local conditions when selecting habitat (Rubio and Carrascal, 1994). The microhabitat features preferred by most snakes in our study (retreat sites, shrubs) were not as clearly related to thermoregulation, and physiological demands clearly did not restrict their use of habitat at a landscape scale. The apparent lack of hierarchical habitat selection seems more likely to be a consequence of fine-grained differences between habitats that allow massasauga rattlesnakes to find suitable microhabitat in all available macrohabitats. Habitat selection at a landscape scale is less likely the more evenly resources are distributed among habitats, because animals would incur costs moving between habitats (time, energy, increased predation risk) for comparatively little benefit in terms of additional resources (Levins, 1962; Bryant, 1973; Morris, 1987). Although more studies are needed to determine whether reptiles generally do not select habitat hierarchically, the results of our study and Rubio and Carrascal (1994) clearly challenge the assumption that hierarchical habitat selection is universal among terrestrial vertebrates (Johnson, 1980; Mackey and Lindenmayer, 2001).

4.3. Implications for conservation

Effective management of eastern massasauga rattlesnake populations on the Bruce Peninsula will require the identification and protection of habitat for foraging, gestation, and hibernation. Of these habitat components, gestation and hibernation sites are the most specialized and should be the focus of efforts to locate and preserve. Because the only significantly avoided habitat during the active season (dense deciduous forest) was the most heavily used for hibernation, the disturbance of any habitat on the Bruce Peninsula has the potential to be detrimental to massasauga populations.

As with other species at risk, a goal of efforts to conserve massasauga rattlesnakes is to extrapolate results of local habitat studies to identify suitable habitat regionally and beyond (pending studies of regional habitat selection and local habitat selection in other parts of the range). Local habitat associations identified through intensive fieldwork can be scaled up using aerial or satellite imagery to identify habitat. For species that select habitat primarily at a microhabitat scale, however, landscape-scale modeling of habitat use will only be effective to the extent that habitats reflect the availability of suitable microhabitats within. Because our study site was character-

ized by high microhabitat heterogeneity within habitats, landscape-scale modeling will identify massasauga rattlesnake habitat with low precision. As the resolution of satellite imagery improves, so to should the ability to distinguish microhabitat features within habitats (e.g., canopy gaps, large rocks) associated with species occurrence. Until such time, habitat modeling for species that do not select habitat at a landscape scale will be problematic.

Note added in proof

Subsequent to acceptance of our article, it came to our attention that two habitat categories were mislabeled on our GIS maps (dense coniferous forest and dense deciduous forest). We re-classified dense deciduous, dense coniferous, and dense mixed forests as a single category (dense forest) and repeated all analyses. This did not alter our general results or conclusions.

Acknowledgements

We thank Frank Burrows, Jessica Calhoun, and the rest of the staff from Bruce Peninsula National Park for their advice and support throughout the study. Brad Toms, Ron Williams, Sean Liipere, Craig McIntosh, Melissa Coady, Andrew Bruce, and Brianna Burley assisted with field work. Comments by Gerardo Carfagno, Michael Libsch, Stephen Mullin, and two anonymous reviewers improved the manuscript. Funds for this project were provided in part by the Parks Canada Species at Risk Recovery Action and Education Fund, a program supported by the National Strategy for the Protection of Species at Risk. Additional funding was supplied by the Interdepartmental Recovery Fund of the Canadian Wildlife Service. Support for D.S.H. was provided by the Department of Natural Resources and Environmental Sciences at the University of Illinois in Urbana-Champaign.

REFERENCES

- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74, 1313–1325.
- Allen, T.F.H., Starr, T.B., 1982. *Hierarchy: Perspectives for Ecological Complexity*. The University of Chicago Press, Chicago.
- Bennet, K.D., 1992. Holocene history of forest trees on the Bruce Peninsula, southern Ontario. *Canadian Journal of Botany* 70, 6–18.
- Bergin, T.M., 1992. Habitat selection by the western kingbird in western Nebraska: a hierarchical analysis. *The Condor* 94, 903–911.
- Blouin-Demers, G., Weatherhead, P.J., 2001a. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82, 2882–2896.
- Blouin-Demers, G., Weatherhead, P.J., 2001b. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82, 3025–3043.
- Bryant, E.H., 1973. Habitat selection in a variable environment. *Journal of Theoretical Biology* 41, 421–429.
- Charland, M.B., Gregory, P.T., 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). *Journal of Zoology* 236, 543–561.
- Clark, R.W., 2004. Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology* 30, 607–617.
- Coady, M., 2005. A distance-based analysis of seasonal habitat use and den site selection for american black bears (*Ursus americanus*) on the Bruce Peninsula, Ontario. Masters Thesis, Trent University, Peterborough, Ontario.
- Cody, M.L., 1985. *Habitat Selection in Birds*. Academic, New York.
- Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species–environment relationships. *Landscape Ecology* 17, 637–646.
- Ford, N.B., Burghardt, G.M., 1993. Perceptual mechanisms and the behavioral ecology of snakes. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Toronto, Ont., pp. 117–164.
- Grand, J., Cushman, S.A., 2003. A multi-scale analysis of species–environment relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) community. *Biological Conservation* 112, 307–317.
- Graves, B.M., Duvall, D., 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. *Journal of Herpetology* 27, 33–41.
- Greene, H.W., 1988. Antipredator mechanisms in reptiles. In: Gans, C., Huey, R.B. (Eds.), *Biology of the Reptilia: Defense and Life History*. Alan R. Liss, New York, pp. 1–152.
- Gutzwiller, K.J., Anderson, S.H., 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. *The Condor* 89, 534–548.
- Harvey, D.S., 2005. Detectability of a large-bodied snake (*Sistrurus c. catenatus*) by time-constrained searching. *Herpetological Review* 36, 413–415.
- Heard, G.W., Black, D., Robertson, P., 2004. Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. *Austral Ecology* 29, 446–460.
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Johnson, G., 2000. Spatial ecology of the Eastern Massasauga (*Sistrurus c. catenatus*) in a New York peatland. *Journal of Herpetology* 34, 186–192.
- Kearney, M., 2002. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. *Journal of Thermal Biology* 27, 205–218.
- Klauber, L.M., 1982. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. Abridged version. University of California Press, Berkeley, CA.
- Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59, 253–260.
- Levins, R., 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *The American Naturalist* 96, 361–373.
- Lourdais, O., Shine, R., Bonnet, X., Guillon, M., Naulleau, G., 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos* 104, 551–560.
- Mackey, B.G., Lindenmayer, D.B., 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography* 28, 1147–1166.
- McLoughlin, P.D., Case, R.L., Gau, R.J., Cluff, H.D., Mulders, R., Messier, F., 2002. Hierarchical habitat selection by

- barren-ground grizzly bears in the central Canadian Arctic. *Ecosystems Ecology* 132, 102–108.
- McLoughlin, P.D., Walton, L.R., Cluff, H.D., Paquet, P.C., Ramsay, M.A., 2004. Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy* 85, 576–580.
- Meffe, G.K., Carroll, C.R., 1997. *Principles of conservation biology*, second ed. Sinauer Associates, Sunderland, Massachusetts.
- Morris, D.W., 1987. Ecological scale and habitat use. *Ecology* 68, 362–369.
- Mullin, S.J., Gutzke, W.H.N., 1999. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). I. Influence of habitat structural complexity when searching for mammalian prey. *Herpetologica* 55, 18–28.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H., 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, New Jersey.
- Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. *The American Naturalist* 137, S29–S49.
- Parent, C., Weatherhead, P.J., 2000. Behavioral and life history response of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. *Oecologia* 125, 170–178.
- Pringle, R.M., Webb, J.K., Shine, R., 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84, 2668–2679.
- Prior, K.A., Weatherhead, P.J., 1994. Response of free-ranging eastern massasauga rattlesnakes to human disturbance. *Journal of Herpetology* 28, 255–257.
- Prior, K.A., Weatherhead, P.J., 1996. Habitat features of black rat snake hibernacula in Ontario. *Journal of Herpetology* 30, 211–218.
- Reinert, H.K., 1984. Habitat variation within sympatric snake populations. *Ecology* 65, 1673–1682.
- Reinert, H.K., 1993. Habitat selection in snakes. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Toronto, Ontario, pp. 201–240.
- Reinert, H.K., Cundall, D., 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982, 702–705.
- Reinert, H.K., Kodrich, W.R., 1982. Movements and habitat utilization by the Massasauga, *Sistrurus catenatus catenatus*. *Journal of Herpetology* 16, 162–171.
- Rettie, W.J., Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23, 466–478.
- Rolstad, J., Loken, B., Rolstad, E., 2000. Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. *Oecologia* 124, 116–129.
- Rubio, J.L., Carrascal, L.M., 1994. Habitat selection and conservation of an endemic Spanish lizard *Algyroides marchi* (Reptilia, Lacertidae). *Biological Conservation* 70, 245–250.
- Seigel, R.A., 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri, USA. *Biological Conservation* 35, 333–346.
- Shine, R., 1995. A new hypothesis for the evolution of viviparity in reptiles. *American Naturalist* 145, 809–823.
- Shine, R., Fitzgerald, M., 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal Eastern Australia. *Biological Conservation* 76, 113–122.
- Shine, R., Sun, L., 2002. Arboreal ambush site selection by pit-vipers *Gloydius shedaoensis*. *Animal Behaviour* 63, 565–576.
- Symanski, J., 1998. *Sistrurus c. catenatus* rangewide status assessment. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota.
- Theodoratus, D.H., Chiszar, D., 2000. Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* 137, 119–135.
- Tsairi, H., Bouskila, A., 2004. Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica* 60, 13–23.
- Weatherhead, P.J., Prior, K.A., 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus c. catenatus*). *Journal of Herpetology* 26, 447–452.
- Webb, J.K., Shine, R., 1997. A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biological Conservation* 82, 203–217.
- Webb, J.K., Shine, R., 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biological Conservation* 86, 233–242.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385–397.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.
- Wright, B.A., 1941. Habit and habitat studies of the massasauga in northeastern Illinois. *American Midland Naturalist* 25, 659–672.