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# WHICH HABITAT SELECTION METHOD IS MOST APPLICABLE TO SNAKES? CASE STUDIES OF THE EASTERN MASSASAUGA (*SISTRURUS CATENATUS*) AND EASTERN FOX SNAKE (*PANTHEROPHIS GLOYDI*)

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***Abstract.*—Successful species conservation is dependent upon understanding that the habitat preferences of species occur on multiple spatial scales; however, effective synthesis of findings between studies can be hindered by the use of different methods. We applied two habitat selection analyses to two sets of snake radiotelemetry data, which led to differences in results. We discuss perceived strengths and weaknesses of each approach and how they can be used in future studies of snakes. Compositional Analysis (CA) is a classification-based approach, while Euclidean Distance Analysis (EDA) is a distance-based approach. Each method detected non-random habitat selection on both the landscape and home range level, indicating that both Eastern Massasaugas (*Sistrurus catenatus*) and Eastern Fox Snakes (*Pantherophis gloydi*) made habitat selection choices at multiple spatial scales. Eastern Massasaugas used a mosaic of habitat types but were consistently associated with forest edge and scrub-shrub wetland, while Eastern Fox Snakes were most often associated with upland edge and old field habitat types. The two methods drew different conclusions, however, and complete understanding of habitat associations may require the use of both methods, taking into account the limitations of each. Compositional Analysis may be more applicable at the landscape level than EDA because of reliance of EDA upon random points, which leads to the identification of unused habitat types (e.g., open water) as preferred by Eastern Fox Snakes. However, at the home range level, EDA was better able to incorporate edge habitats into analyses, a habitat feature likely important for many snake species. We recommend that investigators adopt a combination of these methods, employing CA at the landscape level and EDA on finer scales.**

*Key Words.*—Eastern Fox Snake; Eastern Massasauga; habitat preference; modeling; *Pantherophis gloydi*; *Sistrurus catenatus*

## INTRODUCTION

Habitat loss and fragmentation may constitute the greatest threat to biodiversity (Wilson 1992). Reduction in available living space resulting from habitat loss has direct ramifications for species abundance and diversity. Concern over habitat loss has lead to the advancement of studies from focusing on habitat associations of a species (e.g., Klopfer 1969) to quantitative studies of habitat use that seek to explicate the underlying mechanisms of habitat selection (Reinert 1984a, b; Blouin-Demers and Weatherhead 2001; Moore and Gillingham 2006; Jenkins et al. 2009). Elucidation of the mechanisms and patterns of habitat selection for a species will form the foundation for future management and conservation plans.

Although identification of preferred habitat for a species has become a fundamental practice for promoting wise conservation and management, problems remain with analysis tools and comparisons between studies. Habitat use for a species can be variable over its geographic distribution (Shine 1987; Johnson et al. 2000), occur on multiple spatial or temporal levels (Harvey and Weatherhead 2006), and be influenced by sex, age, or reproductive class (Reinert 1984a, b; Shine and Bonnet 2009; Weatherhead and Madsen 2009). Methods used to discriminate such effects vary between studies, and debate continues concerning the most appropriate method of quantifying habitat selection (Conner and Plowman 2001; Conner et al. 2003; Dussault et al. 2005).

Two robust yet fundamentally different methods of quantifying macrohabitat (i.e., patch) selection have been put forth: Compositional Analysis (CA) and Euclidean Distance Analysis (EDA). Compositional Analysis is a classification based technique, whereas EDA is a recently introduced distance-based alternative to CA. Compositional Analysis relies on classifying animal locations by habitat type and determining proportional use (Aebischer et al. 1993). In contrast to CA, which assigns each animal location to only one habitat class, EDA computes the distance between each animal location and the nearest representative of each habitat type (Conner and Plowman 2001; Conner et al. 2003). Because proximity of each location to each type of landscape feature is known, the approach is explicitly multivariate, and distances to each habitat type represent multiple response variables (Conner and Plowman 2001). Both methods of analysis use the individual animal, not telemetry locations, as the sampling unit, thus avoiding concerns about pseudoreplication. Both can also be used to produce a habitat utilization rank order in which habitats are ranked from most preferred to most avoided.

Identification of the perfect habitat selection assessment method would require knowledge of the "true" habitat association of a species (which we, of course, will never have) by which to judge its performance, leaving us with an unresolvable problem when comparing quantitative methods. Although a definitive answer as to which method is most accurate is not forthcoming, the strengths and weaknesses of each method in different situations can be studied. For example, on coarse spatial scales with a patchy habitat distribution, a distance-based analysis may be hindered by its reliance on random points resulting in perceived selection for all habitat types (Dussault et al. 2005). Furthermore, EDA may identify a habitat that was never used as preferred habitat, often without biological significance (Dussault et al. 2005), because of its proximity to often used habitats. An example given by Dussault et al. (2005) is of a species that strongly prefers burned areas, with habitats surrounding the burned areas erroneously identified as preferred. Compositional Analysis is robust to habitat associations and will rarely identify an unused habitat as preferred on the landscape level and never at the home range scale (Aebischer et al. 1993). Euclidian Distance Analysis may be advantageous in scenarios for which ecotones are frequently used by study animals because it is capable of overcoming the unit-sum constraint (in which the sum of the availability of all habitats must equal one) and categorizing a particular area as two habitat types simultaneously (Conner and Plowman 2001), whereas CA needs each distinct habitat patch to be discretely categorized (Aebischer et al. 1993).

Quantitative studies employing CA have become widespread in the literature (e.g., Pendleton et al. 1998; Conner et al. 1999; Marshall et al. 2006), and EDA based studies have been gaining in popularity (e.g., Perkins and Conner 2004; Menzel et al. 2005). Although these methods have been compared and debated (Conner et al. 2003; Dussault et al. 2005), the comparisons deal with telemetry data from birds and mammals and take place at only one spatial scale. To our knowledge, relatively few studies employing CA have been applied to snakes (but see Harvey and Weatherhead 2006; Marshall et al. 2006; Moore and Gillingham 2006) and no published studies of snakes have used an EDA approach. Large-scale declines in snake populations, often due to habitat loss, render quantitative studies a priority (Dodd 1987; Gibbons et al. 2000). The application of the proper habitat selection analysis at the proper scale will have a direct influence on the quality and applicability of habitat use studies. Here we employ both CA and EDA to study the habitat selection of two imperiled snake species. Our objectives are to provide detailed information about the habitat selection of the Eastern Massasauga (*Sistrurus catenatus*) and the Eastern Fox Snake (*Pantherophis gloydi*) to assess the applicability of each method when applied to these snake data and to make recommendations based upon the performance of each method to facilitate consistency and comparability among future studies.

## MATERIALS AND METHODS

***Study sites and species.***—We tracked the Eastern Massasauga and the Eastern Fox Snake using radiotelemetry at two locations in Michigan, USA in 2006 and 2007. We tracked Eastern Massasaugas in the northern part of the Lower Peninsula near Grayling at an 800-ha parcel of land bordering the Manistee River. The habitat consisted of large patches of scrub-shrub wetland, coniferous and deciduous forest, and managed pine plantation. We studied Eastern Fox Snakes along the Lake Erie shoreline at a managed hunting reserve for waterfowl, which was 273 ha in size. The site was bordered to the east and south by Lake Erie and to the west by residential, agricultural, and fish farm properties.

***Radiotelemetry.***—Using a modification of the procedures of Weatherhead and Anderka (1984), we surgically implanted individuals of each species with temperature-sensitive radiotransmitters (Holohil Systems Ltd., Carp, Ontario, Canada; SI-2T, 9.0 g or SI-2T, 5.0 g). Transmitters did not exceed 5% of a snake's mass. We held snakes for three to five days to ensure recovery from surgery and then released them at their respective capture locations.

We located each study animal at least three times per week during the activity season, from 5 May to 1 September, using a Telonics TR-4 receiver and a handheld H-type antenna (Telonics Inc., Mesa, Arizona, USA). Each time we tracked a snake, we recorded the animal's location using a hand held GPS unit (Garmin GPS III, Garmin Inc., Olathe, Kansas, USA). If a snake had not moved between successive tracking events, we included the same location in analyses multiple times (once for each time the animal was located in that position). We recorded the macrohabitat type in which the snake was found. We did not use triangulation for locating Eastern Massasaugas, and only rarely (7% of locations) used it for locating Eastern Fox Snakes when locations were in habitat patches into which we could not penetrate.

We plotted snake locations on aerial photographs of the study sites using ArcMap 9.2 (ESRI, Inc., Redlands, California, USA). We calculated home ranges using the 100% Minimum Convex Polygon (MCP) method (Mohr 1947; Jehnrich and Turner 1969). We used bootstrap

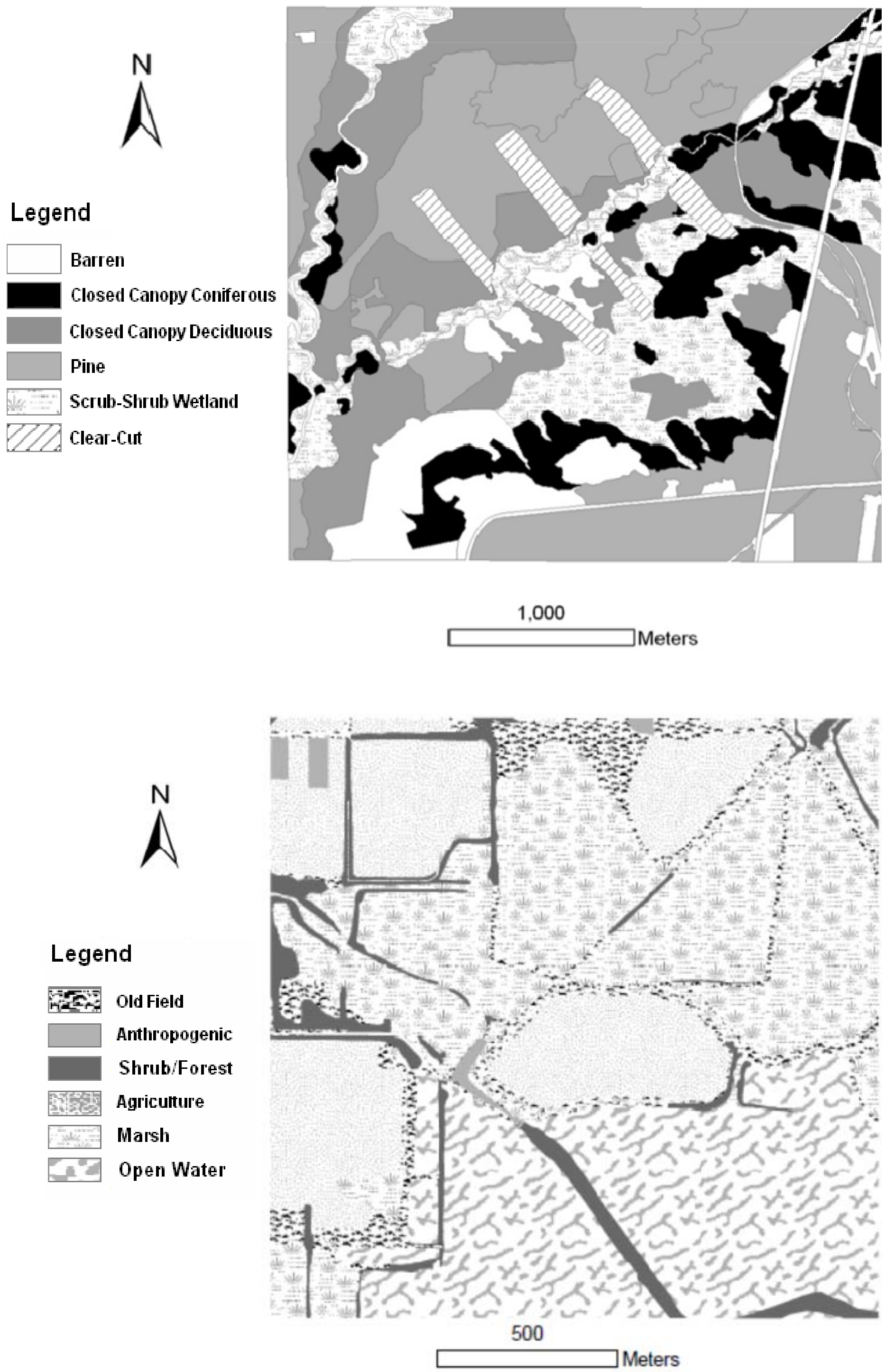


**FIGURE 1.** Macrohabitat map for the study sites at Grayling (top) and Erie (bottom) Michigan, USA. Descriptions of each habitat type can be found in Table 1.

analysis to ensure that the number of relocations per animal was sufficient to accurately measure home range size (Robertson et al. 1998).

***Habitat delineation.*****—**We defined macrohabitat by both soil hydrology and land cover. Using aerial photos (http://seamless.usgs.gov; accessed January 2006), we identified and delineated habitat types throughout the study sites. We used ArcMap 9.2 to digitize the patches of each available habitat type. Extensive ground truthing was used to validate habitat delineation and accuracy of boundaries. We identified seven habitat types at Grayling (Fig. 1), including barrens (BA), coniferous forest (CF), deciduous forest (DF), pine forest (PN), forest edge (FE), scrub shrub (SS), and clear-cut (CL; full descriptions of each habitat type can be found in Table 1).

We also identified seven habitat types at Erie (Fig. 1), including old field (OF), anthropogenic (AN), shrub/forest (SF), agriculture (AG), marsh (MA), upland edge (UE), and open water (OW; Table 1).

***Analysis of habitat selection.*****—**We analyzed habitat selection on two spatial scales. Landscape level selection refers to habitat use within MCPs compared to their availability across the study site (second order selection, Johnson 1980), and home range habitat selection refers to the proportionate use of habitats compared to their availability within the boundaries of that individual's MCP (third order selection, Johnson 1980). We applied both CA and EDA at each spatial scale. Although no direct quantitative comparison between the two methods was possible due to lack of knowledge about "true" habitat preferences of any species, we discuss differences in the conclusions of each method and discuss applicability of each method to snake telemetry data. When a method detected non-random habitat use, we evaluated the ability to make distinctions between preference and avoidance based upon the pairwise rank orders of habitat utilization produced.

***Compositional analysis.*****—**We analyzed landscape level habitat use by dividing the proportional area of each habitat type within an individual MCP by the proportional area of each habitat type within the study site. Usage for landscape analysis was defined by the home range (MCP), while availability was defined by the proportion of habitats within the study site. We delineated the study site itself by digitizing an MCP that included all telemetry locations. We also used CA to examine home range level habitat use by comparing the composition of habitats used by the snakes in their home ranges to the habitat composition of their home ranges. We performed area calculations in ArcMap 9.2 with the Hawth's Analysis Tools extension (Beyer, H.L. 2004. Hawth's Analysis Tools for ArcGIS. Available from http://www.spatialecology.com/htools.) We analyzed the data using SAS 9.1 (SAS Inc., Cary, North Carolina, USA) with the program extension Bycomp, a Compositional Analysis tool.

Using CA, we analyzed Eastern Fox Snake data twice; once including upland edge as a distinct habitat type and once with it excluded. An assumption of CA is that the sum of all available habitats must equal one (the unit-sum constraint described by Aebischer et al. 1993). To include edge as a distinct habitat, the two adjoining habitats must be reduced in size to accommodate creation of the new "edge" habitat. Because shrub/forest and old field habitats often occur as small patches near water's edge at Erie, their area is significantly reduced when upland edge is delineated for analysis. The analysis of data in both ways allowed us to evaluate the use of edge habitat via CA and to monitor the effect this approach has on the perceived use of habitats that occur in small patches.

**TABLE 1**. Available macrohabitats for Eastern Massasaugas (*Sistrurus catenatus*) and Eastern Fox Snakes (*Pantherophis gloydi*) at the Grayling and Erie study sites in Michigan, USA during 2006 and 2007.

| Habitat Type | Code | Description | Location |
|---|---|---|---|
| Scrub-shrub | SS | Less than 30% canopy cover dominated by scattered shrubs | Grayling |
| Barrens | BA | No canopy with ground cover dominated by lichen and blueberry | Grayling |
| Pine forest | PN | Forest dominated by Red (*Pinus resinosa*) or Jack Pine (*P. banksiana*) | Grayling |
| Deciduous forest | DF | Greater than 50% canopy dominated by oak, maple, or aspen | Grayling |
| Coniferous forest | CF | Greater than 50% canopy dominated by spruce or cedar | Grayling |
| Clear-cut | CL | No canopy, logged during winter 2006 | Grayling |
| Forest edge | FE | 15 m interface between an open and a forested habitat | Grayling |
| Old field | OF | Dominated by grasses and forbs | Erie |
| Anthropogenic | AN | Areas modified by humans such as mowed areas, yards, and homes | Erie |
| Shrub/forest | SF | Greater than 30% canopy cover | Erie |
| Agriculture | AG | Active farmland | Erie |
| Marsh | MA | Aquatic habitat with emergent vegetation and less than 2 m deep | Erie |
| Open water | OW | Aquatic habitat devoid of emergent vegetation and deeper than 2 m | Erie |
| Upland edge | UE | 15 m of terrestrial habitat adjacent to marsh or open water | Erie |

***Euclidean distance analysis.***—For landscape analysis we generated 5000 random points across each study site and 1000 random points within the MCP of each snake. For each snake location, we determined the distance to the nearest patch of each habitat type and then did the same for each randomly generated point. While the random locations within an MCP were bounded by the MCP, the distance to the nearest habitat type was calculated for the nearest patch, regardless of whether the patch was within the MCP. These calculations were performed in ArcMap 9.2 using Hawth's Analysis Tools and ET GeoWizards 9.7 (ET Spatial Techniques, Pretoria, South Africa) extensions. We performed home range analysis by determining the distance from each snake location to each habitat type and comparing that to the distances obtained from random points within an individual's MCP. For each individual, we calculated the mean distance to each of the available habitat types for snake locations and random points. For landscape habitat analysis, the mean distance to each habitat type from random locations within an MCP ($r_i$) was divided by the mean distance to each habitat type from random locations within the study site ($s_i$). For home range habitat analysis, the mean distance from snake locations to each habitat type was calculated ($u_i$) and subsequently divided by $r_i$ (for a more detailed description see Conner and Plowman 2001).

We used a Multivariate Analysis of Variance to compare landscape and home range distance ratios (landscape distance ratio = $r_i/s_i$, home range distance ratio = $u_i/r_i$) to the value one to determine if habitats were preferred, avoided, or used randomly. The null hypothesis that habitat use was random was rejected if the distance ratios differed significantly from one. We then used pairwise t-tests to compare whether one habitat was preferred over another habitat; that is to say, habitats with a ratio statistically less than a second habitat were preferred over that second habitat (Conner et al. 2003). For all analyses, alpha levels were set at 0.05 and all data were first tested for normality using Kolmogorov-Smirnov tests.

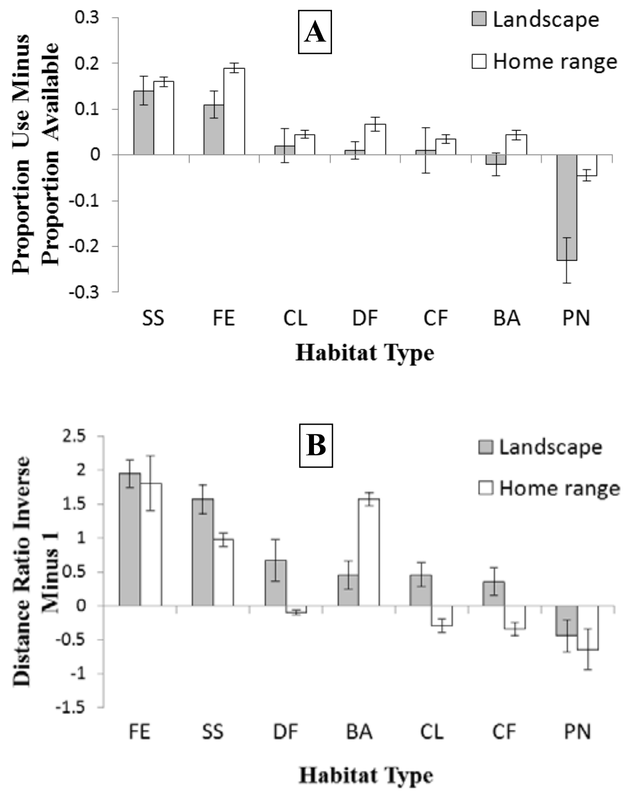


**FIGURE 2.** Relative use vs. availability (± 1 SE) of habitat types on two spatial scales for the Eastern Massasauga (*Sistrurus catenatus*) near Grayling, Michigan, USA by (A) Compositional Analysis and (B) Euclidean Distance Analysis.

## RESULTS

We tracked 36 Eastern Massasaugas and 23 Eastern Fox Snakes throughout the study. Based upon results from bootstrap analyses, we excluded snakes tracked fewer than 25 times or for durations of less than 60 days from habitat selection analyses. We obtained an average of 57 ± 2 relocations (range = 28–75) per snake. Individual snakes tracked in multiple seasons had one season randomly excluded to avoid pseudoreplication. Overall, we included 29 Eastern Massasaugas and 18 Eastern Fox Snakes in subsequent habitat selection analyses.

***Compositional analysis.***—Compositional Analysis detected non-random habitat selection at the landscape level for Eastern Massasaugas (Fig. 2a; $\lambda = 0.101$, $P < 0.001$). Forest edge was the most preferred habitat type. Scrub-shrub, deciduous forest, and coniferous forest were equally preferred (Table 2). Barrens were ranked above clear-cut and pine, which were ranked last. Compositional Analysis detected mild habitat selection for Eastern Massasaugas at the home range level ($\lambda = 0.615$, $P = 0.051$). No significant preference was detected between scrub-shrub, barrens, forest edge, coniferous forest, or clear-cuts (all $P > 0.50$). Deciduous forest and pine forest, respectively, were ranked last.

At the landscape level for Eastern Fox Snakes, CA detected significant non-random habitat use (Fig. 3a; $\lambda = 0.154$, $P < 0.001$), with preference for upland edge over each of the other habitat types (Table 2). Marsh was preferred over anthropogenic and agricultural. All other comparisons were non-significant ($P > 0.25$). Selection was also non-random ($\lambda = 0.02$, $P < 0.001$) at the home range level, with upland edge being preferred over each of the other habitats. Old field, anthropogenic, and shrub/forest habitats were each preferred over agricultural, marsh, and open water habitats ($P < 0.05$).

**TABLE 2**. Relative rank orders of habitat utilization based on results from Compositional Analysis (CA) and Euclidean Distance Analysis (EDA) for Eastern Massasaugas (*Sistrurus catenatus*) and Eastern Fox Snakes (*Pantherophis gloydi*) in Michigan, USA. Habitats that share an underline were equally preferred or avoided based on pairwise t-tests ($P < 0.05$). Habitat acronym definitions are in Table 1.

| | Preferred ⟷ Avoided |
|---|---|
| **Eastern Massasauga** | |
| Landscape CA | FE SS DF CF BA CL PN |
| Landscape EDA | FE SS DF CL BA CF PN |
| Home Range CA | SS CL PN BA FE DF CF |
| Home Range EDA | FE BA CF CL SS PN DF |
| **Eastern Fox Snake** | |
| Landscape CA | UE MA OW OF SF AG AN |
| Landscape EDA | UE OW MA OF AG AN SF |
| Home Range CA | UE OF AN SF MA AG OW |
| Home Range EDA | UE OF AN SF MA OW AG |
| Home Range CA (No Edge) | OF AN SF AG MA OW |
| Home Range EDA (No edge) | OF AN AG SF MA OW |

Marsh was preferred over open water ($P < 0.001$). All other comparisons were non-significant. When upland edge was excluded from analysis, habitat selection was still non-random at the landscape level (Fig. 4; $\lambda = 0.29$, $P = 0.004$) and the activity range level ($\lambda = 0.03$, $P < 0.001$). At the landscape level, old field, anthropogenic, and shrub/forest were equally preferred over all other habitat types. At the home range level, old field and anthropogenic became the most preferred habitat types with shrub/forest, marsh, and open water being equally avoided.

***Euclidean distance analysis.***—Euclidean Distance Analysis detected non-random Eastern Massasauga habitat selection at the landscape level (Fig. 2b; $F_{7,22} = 125.65$, $P < 0.001$). Snake locations within home ranges were significantly closer to forest edge, scrub-shrub, deciduous forest, barrens, clear-cuts, and coniferous forest than random points ($P < 0.05$). Forest edge was preferred over all other habitat types except scrub-shrub ($P < 0.05$). Pine forest was least preferred. Euclidean Distance Analysis also detected non-random habitat selection at the home range level ($F_{7,22} = 280.18$, $P < 0.001$). Snake points were closer to forest edge, scrub-shrub, and barrens than expected ($P < 0.05$) and farther from all other habitats than from random points.

Habitat selection at the landscape level for Eastern Fox Snakes was non-random (Fig. 3b; $F_{6,17} = 3.26$, $P < 0.001$). Upland edge was preferred over anthropogenic, shrub/forest and agricultural habitats. There was no evidence that upland edge was preferred over old field, marsh, or open water (all $P > 0.12$). Open water was preferred over shrub/forest ($P = 0.02$). All other comparisons were non-significant ($P > 0.05$). At the home range level, habitat selection was non-random ($F_{6,17} = 5.26$, $P < 0.001$), with Eastern Fox Snakes preferring upland edge and old field equally. Additionally, upland edge and old field were each preferred over the remaining habitats (Fig. 3b). Anthropogenic habitat was preferred over agricultural, and all other comparisons were non-significant.

## DISCUSSION

We detected non-random habitat selection by two different methods for both Eastern Massasaugas and Eastern Fox Snakes in Michigan. We found that both species preferred a mosaic of habitat types at both the

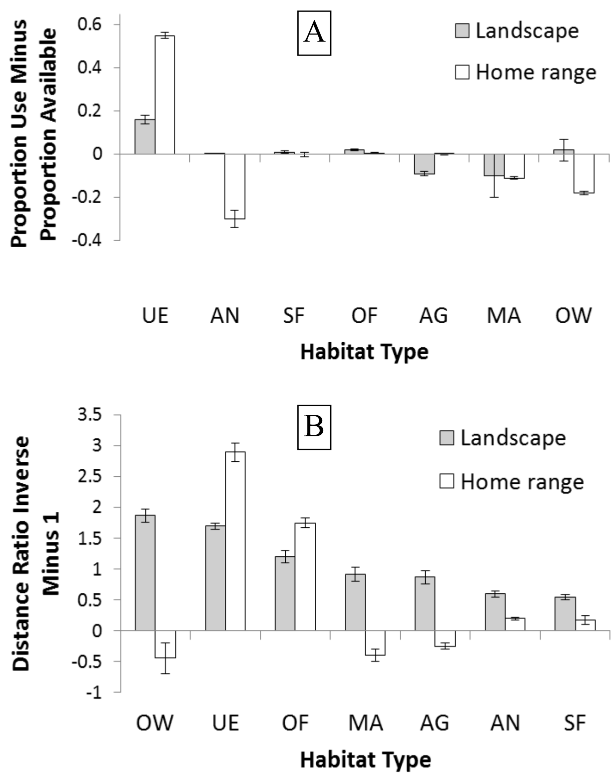


**FIGURE 3.** Relative use vs. availability (± 1 SE) of habitat types, (including edge habitat) on two spatial scales for the Eastern Fox Snake (*Pantherophis gloydi*) near the Lake Erie shoreline, Michigan, USA by (A) Compositional Analysis and (B) Euclidean Distance Analysis.

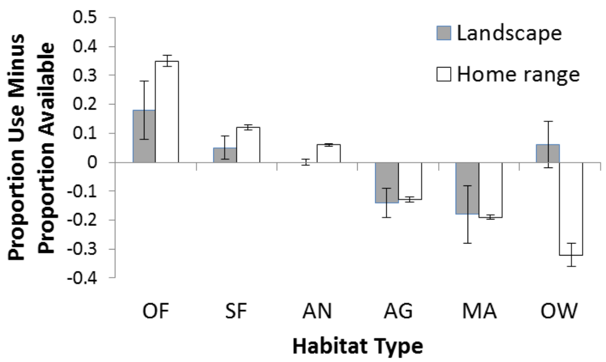


**FIGURE 4.** Relative use vs. availability (± 1 SE) of habitat types, (excluding edge habitat) on two spatial scales for the Eastern Fox Snake (*Pantherophis gloydi*) near the Lake Erie shoreline, Michigan, USA, by Compositional Analysis.

landscape and home range levels of analyses. The Eastern Massasauga was most often associated with forest edge and scrub-shrub wetland, although on the landscape level, all available habitat types except pine forest were used proportionately more than their availability. Eastern Fox Snakes were most often associated with upland edge and old field habitats although, depending on the analysis method, anthropogenic habitat was preferred. Habitat selection for the Eastern Massasauga was strongest at the landscape level, while for Eastern Fox Snakes habitat associations were strong at both spatial scales. Evidence indicates that both species make habitat choices at multiple spatial scales and use a heterogeneous mix of habitat types, with one or two habitat types used more than others.

An understanding of the habitat preference of these two snake species will be influenced by the method by which the data were analyzed. When applied to two years of tracking data for Eastern Massasauga and Eastern Fox Snakes, CA and EDA both detected non-random habitat selection in all scenarios, indicating that both species are making habitat selection choices on multiple spatial scales. However, we believe that the two methods do not perform equally well at different spatial scales for both species.

At the landscape level, we believe that CA may be more useful than EDA. Compositional Analysis produced a meaningful and biologically relevant (based upon the observations of the authors) rank order of habitat utilization. Distance-based analysis was hindered at the landscape level by its reliance on random points. When used in a patchy landscape such as Erie, random points can often indicate equal preference or avoidance for all habitat types (Dussault et al. 2005). For example, for Eastern Fox Snakes, EDA indicated that most habitat types were preferred with few differences among them, including open water, a habitat type in which Fox Snakes were never observed. For Eastern Massasaugas, the rank orders of habitat utilization produced by EDA and CA were very similar, although EDA was unable to distinguish statistical differences between habitat types. Conversely, CA detected non-random habitat selection with both sets of data and was able to make meaningful preference and avoidance utilization ranks.

A further shortcoming of EDA is that it can identify a habitat that was never used as preferred habitat (Dussault et al. 2005). An example given by Dussault et al. (2005) is of a species that strongly prefers burned areas, with habitats surrounding the burned areas erroneously identified as preferred. Using simulated radio-tracking data in a variety of scenarios, Dussault et al. (2005) found that EDA was often unable to distinguish between preferred and avoided habitats when the two habitat types occurred in proximity to one another. This was apparent for Eastern Fox Snakes, as both open water (in which a snake was never located) and marsh (in which snakes were seldom located) were identified as preferred habitat types by EDA at the landscape level. This is also evident at Grayling, where EDA ranked clear-cut (a seldom-used habitat) equally with scrub-shrub (an often-used habitat) based upon the proximity of clear-cuts to habitats used more often. Before application of EDA, researchers should be aware of spatial relationships between habitat types that might confound results. Euclidean Distance Analysis may be unusable or must be adjusted to exclude habitats that could be erroneously identified as preferred, without actually being used due to their proximity to preferred habitats. Compositional Analysis is robust to habitat associations and will rarely identify an unused habitat as preferred on the landscape level and never at the home range scale.

In one scenario, CA failed to make distinctions among habitats at the home range level. Mild non-random habitat selection in home ranges was indicated at Grayling by CA; however, no distinctions were made among six of the seven habitats identified as preferred. Thus, although this method indicated that habitat selection was non-random, few meaningful distinctions were made among the habitats, providing little to no insight into habitat use patterns of this snake species. Pine forest, a habitat used less frequently than its availability, was ranked equally with scrub-shrub, an often-used habitat. Euclidean Distance Analysis was more successful at distinguishing preference and avoidance between habitats at this level of analysis as it identified forest edge and barrens as the preferred habitat types, coniferous forest as being used equivalent to its availability, and the other habitats as equally avoided. Conversely, at Erie, EDA and CA produced similar rank orders of habitat utilization with the minor difference of open water ranked slightly higher by EDA than by CA. At Erie, both CA and EDA were effective at this spatial scale.

For a variety of reasons (e.g., thermoregulatory

**Table 3**. Perceived strengths and weaknesses of two habitat selection analyses based on results from this study and those discussed by Aebischer et al. (1993), Conner et al. (2003), and Dussault et al. (2005). Note: plus and minus signs denote high (+), very high (+ +), low (-), and very low (- -) values.

| | Classification based approach (Compositional Analysis) | Distance based approach (Euclidean Distance Analysis) |
|---|---|---|
| "Individual" used as the sampling unit | + + | + + |
| Free of the unit-sum constraint | - - | + + |
| Allows analysis on multiple spatial scales | + + | + + |
| Multiple values associated with each telemetry point | - - | + + |
| Takes into account habitat patch size | - - | + + |
| Robust to telemetry error | - - | + |
| Incorporates edge habitat | + | + + |
| Necessitates use of random points | + + | - - |
| Infers use and avoidance in a patchy landscape | + + | - - |

benefits, prey abundance, etc.), snakes are often associated with edge habitats (Blouin-Demers and Weatherhead 2001; Carfagno et al. 2006; Weatherhead and Madsen 2009). An advantage of EDA is its capability to overcome the unit-sum constraint and to categorize a particular area as two habitat types simultaneously (Conner and Plowman 2001), whereas CA requires that each distinct habitat patch be discretely categorized (Aebischer et al. 1993). This becomes problematic when incorporating habitat edge into analyses (Conner et al. 2003). For instance, when using CA at Erie, we had to redefine linear pieces of old field and shrub/forest habitat as a new, discrete habitat called upland edge. This decreased the availability of old field and shrub/ forest habitats in the analysis, and led to CA identifying only upland edge as a preferred habitat. Euclidean Distance Analysis allows consideration of a habitat as both edge and original habitat simultaneously. At the home range level, this proved to be a valuable approach and led to detection of preference not only for edge habitat but also for shrub/forest and old field. We believe this is an important advantage of EDA over CA as both the Eastern Fox Snake and the Eastern Massasauga showed preference for edge habitat at both spatial scales. This has applicability for researchers trying to distinguish preference and avoidance for habitats that could simultaneously fall into several categories (e.g., burned and unburned habitat types, rivers through different habitat types, and different forestry methods applied to one habitat type).

Understanding habitat selection across multiple scales (Sperry and Weatherhead 2009) and across the geographic range of a species (Shine 1987) is essential to successful conservation. Consistency of methodology among studies will facilitate synthesis of results and allow for a better understanding of the ecology and habitat requirements of a species. Based upon the perceived strengths and weaknesses of each habitat selection method (Table 3), we suggest that researchers would benefit from application of a combination of the methods. Compositional Analysis works well at the landscape level, where it identifies preferred and avoided habitats based upon the proportion of each habitat included within an individual's home range compared to availability across the landscape. It works well within patchy landscapes regardless of spatial associations between habitat types. However, on finer scales EDA may be advantageous for its ability to overcome the unit-sum constraint, allowing habitat types to be categorized two ways simultaneously. This may be valuable for species using edge habitats. The best approach to quantifying habitat selection of snakes will likely be site and species specific. We recommend application of CA on broad spatial scales, especially if the landscape is a patchy mosaic with certain habitats spatially linked to others. On finer scales, EDA may be more consistent in its ability to distinguish preference among habitat types and has the advantage of allowing the simultaneous classification of a habitat multiple ways, allowing unique quantification of habitat edge use. Thus, although choosing the best habitat selection method is site- and species-specific, we suggest that a combination of the two methods at different spatial scales is the best approach to quantifying habitat selection for snakes.

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**ERRATUM.**–a formatting error caused insertion of a blank page in the manuscript. This was removed and the associated text errors corrected. The primary content of the manuscript did not change. (Corrected 22 June 2012 by Malcolm L. McCallum, Managing Editor).