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Impacts of Invasive Plants on Resource Selection and Thermoregulation by the Northern Copperhead (Agkistrodon contortrix mokasen)

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For the degree of Master of Science

Is approved by the final examining committee:

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For the degree of Master of Science

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IMPACTS OF INVASIVE PLANTS ON RESOURCE SELECTION AND THERMOREGULATION BY THE NORTHERN COPPERHEAD (*Agkistrodon contortrix mokasen*)

A Thesis
Submitted to the Faculty
of
Purdue University
by
Evin T. Carter

In Partial Fulfillment of the
Requirements for the Degree
of
Master of Science

August 2012
Purdue University
Fort Wayne, Indiana

For my brothers, Jance and Jerrad.

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ABSTRACT

Carter, Evin T. M.S., Purdue University, August 2012. Impacts of Invasive Plants on Resource Selection and Thermoregulation by the Northern Copperhead (*Agkistrodon contortrix mokasen*). Major Professor: Bruce A. Kingsbury.

Conservation management for any wildlife species relies on an understanding of habitat use and spatial patterns with an increasing need to identify the anthropogenic factors affecting populations (Sanderson *et al.*, 2002). In order to understand those anthropogenic factors, it is generally necessary to first gain an understanding of the basic resource use patterns exhibited by the population(s) of interest. The Northern Copperhead (*Agkistrodon contortrix mokasen*) is a medium sized North American pit-viper (Family Crotalidae) occurring throughout most of the eastern United States. Populations are thought to be stable throughout the majority of its range, but it holds protected status in three states and appears to be experiencing localized declines in some portions of southern Indiana. Copperheads are facing many of the same stressors causing global declines in other reptiles, including habitat loss and degradation, intentional killing and harvesting, as well as the introduction and proliferation of exotic invasive species (Gibbons *et al*., 2000). However, particular causes for declines in the Midwest are currently unknown given that the Northern Copperhead is a relatively understudied species. A limited number of studies pertaining to habitat use by copperheads of any subspecies exist (but see: Fitch, 1960, Reinhert, 1984, Smith *et al.*, 2009), and no radiotelemetric studies have ever investigated habitat use by copperheads in the Midwest.

From June 2008 – November 2011, I radiotracked 22 copperheads at Clifty Falls State Park in Jefferson County, Indiana and nine copperheads at Clark State Forest at the border of Clark, Scott, and Washington County, Indiana. I present data herein on habitat use by each of these populations as well as some of the anthropogenic factors affecting the Clifty Falls State Park population, which appears to be experiencing rapid

decline. I place an emphasis on the consequences of exotic plant invasions at Clifty Falls State Park and the implications and efficacy of mitigation techniques.

In Chapter One, I present data on general habitat use by copperheads at Clifty Falls State Park and Clark State Forest, which represent two geographically separated populations utilizing distinct habitat types. These habitats include oak-hickory ridges across the western portion of the Indiana copperhead range (*e.g.*, Clark State Forest) and rocky gorges and canyons (*e.g.*, Clifty Falls State Park) in the eastern portion where populations appear to be experiencing the greatest declines. Copperheads at Clark State Forest exhibited preference for forest macrohabitats while snakes at Clifty Falls State Park preferred a wider variety of habitats and appeared to exhibit avoidance of forest macrohabitats. A closer investigation into particular forest types at Clifty Falls State Park, however, revealed that each population exhibits preference for dry-upland forest and uses similar habitat when considering availability. Regression models also indicate few differences in microhabitat selection by each population, with snakes at both sites selecting habitats with lower canopy closure, higher leaf litter depth, and in closer proximity to native shrubs compared to random locations. Overall, the results of this study indicate the importance of multi-scale habitat use studies when attempting to determine important resource selection parameters for wildlife.

In Chapter Two, I demonstrate the influence of exotic plants on resource selection as well as the thermal limitations imposed by particular exotic plant species on copperheads at Clifty Falls State Park. Copperheads exhibited clear avoidance of most exotic plant species at multiple spatial scales, with exotic shrubs having the greatest influence on copperhead habitat selection. Avoidance of most exotic plants appears to be at least partially attributable to limited thermoregulatory opportunities within exotic-dominated habitats relative to native habitats, with exotic shrub habitats providing the lowest thermal quality as a group. Additional mechanisms underlying avoidance may include lack of suitable cover and/or decreased prey availability, but their significance is currently unclear. Careful planning and implementation of habitat restoration efforts in invaded habitats should benefit ectotherms in general. As exotic shrubs appear to exhibit the greatest influence on habitat use as well as the greatest impact on thermoregulation, management efforts for snakes and other ectotherms may receive the greatest return by targeting exotic shrubs when multiple species/types of invasive plants are present, although the current and potential risk that several non-shrub species present may be of equal or greater significance for different species or separate populations.

In Chapter Three, I address nonrandom use of artificial forest (recreational) gaps by copperheads at Clifty Falls State Park by simulating closure (to the public) of artificial gaps using ArcGIS. Results from this study demonstrate that by restricting human access to artificial forest gaps, encounters with Northern Copperheads could be reduced by 1.5 – 10 x the expected potential. I discuss results in terms of management implications and provide suggestions for land managers facing related concerns of human-wildlife encounters.

Finally, in Chapter Four I provide direct evidence of the impacts of property management and restoration activities copperheads in southern Indiana, showing that several managed habitats can and do attract copperheads and simultaneously place them at greater risk of injury and/or mortality. At the same time, however, management activities create or maintain forest gaps, providing thermoregulatory opportunities in an otherwise low quality landscape. I discuss my results in terms of the ecological trap concept and provide management recommendations that should be applicable to additional Northern Copperhead populations as well as to other forms of wildlife.

Overall, copperheads in southern Indiana will benefit from control of exotic invasive plants that overtake basking areas, gestation sites, foraging sites, and hibernacula. Large-scale mechanical means of exotic vegetation removal, while effective in eliciting positive responses by copperheads and providing thermally advantageous habitat, should be avoided during periods of time when copperheads and other forms of wildlife are likely to be present. Baseline habitat use data in conjunction with known anthropogenic influences suggests that smaller-scale, ‘softer,’ habitat restoration techniques will be most beneficial to copperheads when they occur in former glades and glade-like areas, grasslands, and thinner-canopy upland (oak-hickory) forest away from public access. These habitats provide important gestation sites and foraging habitats that appear to be at relatively high risk of exotic plant invasions and other anthropogenic impacts.

CHAPTER ONE

HABITAT USE BY NORTHERN COPPERHEADS IN TWO DISTINCT PHYSIOGRAPHIC REGIONS OF SOUTHERN INDIANA

Introduction

The Northern Copperhead (*Agkistrodon contortrix mokasen*) is a medium-sized North American pit-viper (Family Crotalidae) occurring from Connecticut westward through southeastern Iowa and south to northern Alabama and the upper half of Georgia. It is thought to be stable throughout most of its range but is considered "Endangered" in Massachusetts and Iowa and a "Species of Special Concern" in New Jersey. In Indiana, copperheads are confined primarily to the southern hills and canyons region, which includes most of the area north of the Ohio River extending throughout the Knobstone Escarpment to the southern border of the Central Till Plains (Minton, 2001). It occupies dry to dry-mesic upland forest consisting of oak-hickory ridges across the western portion of its Indiana distribution, and populations in the eastern portion are at least partially divided from western populations by an area of lowland (*i.e.*, the Scottsburg Lowlands). East of this lowland and at no significant elevation gain, copperheads occupy rocky canyons and gorges (Minton, 2001; Carter, unpublished data), which are essentially the result of geologic downcutting by streams into the already low-elevation bedrock along the Ohio River Valley (Hill, 1998). Populations in this eastern portion occur at lower abundance with a patchier distribution and appear to be experiencing at least localized declines (Carter, unpublished data; Pers Comm: Dick Davis, Indiana Department of Natural Resources).

To address Northern Copperhead declines and provide conservation management guidelines, I investigated general habitat use and spatial patterns in each of the southern Indiana habitats discussed above, which differ in both physiography and local plant community composition. Since populations in the eastern canyons and gorges appear to be experiencing greater declines and represent a smaller portion of Indiana copperhead populations, I focused most of my efforts on a population in this region. The primary goals for this study were to provide a broader understanding of copperhead ecology and generate baseline habitat use data for subsequent investigations into anthropogenic factors such as exotic plant invasions that appear to be affecting copperheads. Finally, since one my goals for this study was to provide further insights into the general ecology of an understudied species, I also discuss observations of behavior and habitat use I feel are relevant to management and/or may present interesting points for additional research. (More applied results and management recommendations from this study are included later in Chapter Three and Chapter Four.)

Methods

Study Sites

This study occurred from late June 2008 – November 2011 at Clifty Falls State Park (and area immediately adjacent) in Jefferson County, Indiana and at Clark State Forest at the border of Clark, Scott, and Washington Counties in Indiana from April to November 2009. Clifty Falls State Park is an approximately 570-hectare state-owned park in the Muscatatuck Flats and Canyons region of southeastern Indiana and represents the eastern portion of Indiana copperhead habitat. It is characterized by limestone canyons, talus slopes, and mixed deciduous primary and secondary growth forest with public use sites and hiking trails interspersed throughout. The park is bordered on the south by the Ohio River and is essentially an island of semi-natural landscape within the city of Madison, Indiana. Clark State Forest, on the other hand, is located in the Knobstone Escarpment section of the Norman Upland, an area characterized by steep ridges and valleys dominated by old-growth oak-hickory forest. Clark State Forest is representative of the primary habitat utilized by copperheads in Indiana.

Radiotelemetry and Site Characterization

I captured copperheads opportunistically by active search and night road surveys throughout each season with the majority of captures occurring in April and May. Each snake was outfitted with a temperature sensitive Holohil model SB-2T transmitter

(Holohil Systems Ltd., Carp, Ontario) following surgical procedures adapted from Reinert and Cundall (1982) and using isoflurane as an anesthetic. I made an effort to outfit an equal proportion of adult males, nongravid females, and gravid females, and the 5 gram transmitter never exceeded 2.5% of a snake's body mass. Snakes were outfitted within three days of capture and released within one week of their initial capture date. Most surgeries took place during May of each year, and no surgery took place after September 15 of any year in order to reduce the possibility of snake mortality associated with late-season transmitter implantations (Rudolph *et al*., 1998).

Each snake was located an average of three times per week during the active season (early May – October) and opportunistically during the inactive season using a handheld telemetry receiver. I recorded the following data at each snake location: longitude and latitude coordinates (using a handheld GPS), canopy cover (using a spherical densiometer), distance to and diameter at breast height (DBH) of nearest overstory tree (>7.5 cm DBH) and understory tree (< 7.5 cm DBH), distance to nearest herbaceous ground cover, native shrub (woody understory), rock, log (> 7.5 cm in average diameter), and leaf litter, as well as leaf litter depth. Additionally, I recorded macrohabitats as forest, grassy field, glade, talus, anthropogenic, or other though a combination of national land cover data and ocular estimation in the field. I considered forest to be composed predominantly of native overstory trees. Grassy field was defined as being predominantly herbaceous ground cover and lacking abundant woody vegetation. These areas were not mowed or altered regularly. Glades were defined as south to southwest facing slopes composed primarily of rocky substrates with intermittent vegetation and intense sun exposure (lacking overstory and midstory canopy cover). Talus was defined as consisting of rocky talus but lacking intense sun exposure. Anthropogenic was defined as any site with constant human disturbance. Examples included mowed yards, residential areas, roads, and recreational forest gaps. For each snake location, I recorded equivalent data at a site situated 20 meters away in a random direction, giving an equal number of snake locations and comparable random locations (control sites).

Statistical Analyses

Macrohabitat use was examined at both the landscape and activity range level using compositional analysis (Aebischer *et al.* 1993). The landscape level compares proportional macrohabitat availability within the entire study area to proportional habitat use by each individual snake. Macrohabitat use at the activity range level, sometimes referred to as the home range level, provides a more rigorous analysis of use versus availability and was tested by comparing proportional habitat use by each snake to the availability of macrohabitats within each respective snake's activity range. I determined the bounds of each study site by calculating a minimum convex polygon (MCP) around the combined locations of all study subjects at each site. Similarly, I used the MCP approach to define the activity range of each snake. Due to the relative simplicity of habitat categories (forest, grassy field, glade, talus, and anthropogenic) and the size of the study areas, habitats were mapped using aerial photographs and later ground-truthed. Snake locations were plotted in ArcMap, and polygons of habitats were created to determine use and availability. The software Compos Analysis 6.2 (Smith Ecology Ltd.) was then used to run the compositional analysis (Smith, 2005).

I further explored forest utilization by copperheads at Clifty Falls State Park due to the park's more heterogeneous habitat. I mapped habitats in the field by categorizing 550 random survey plots across the study area as dry-upland forest, dry-mesic upland forest, mesic upland forest, grassland (field), talus, glade, or anthropogenic. Definitions for community types can be found in Faber-Langendoen, 2000. I used a hybrid mapping approach by employing a natural neighbor interpolation of forest habitats using the Spatial Analyst in ArcMap 10 (ESRI, 2010). I used non-forest habitats as barriers during the interpolation. The resultant raster was then reclassed to include only the original, discrete, data values and was subsequently converted to a polygon layer. Habitat maps from the previous compositional analysis were then overlaid onto the forest community layer and then clipped and merged accordingly. This produced a map identical to the previous map for Clifty Falls State Park but with forest divided into distinct types, *i.e.*, dry-upland, dry-mesic upland, and mesic upland. I then performed a compositional analysis as before.

Based on a perceptible relationship between copperhead locations at Clifty Falls State Park and edge habitat, I selected to further explore this aspect as well. I generated 2000 random locations in ArcMap and randomly selected an equivalent number of locations from each individual snake for comparison. I then measured the distance to nearest edge habitat from each snake location and random location. Edge habitat was defined as any border between an area of mid to overstory canopy and an area which lacked canopy. I used Chi-Square to determine if a nonrandom relationship existed by comparing the proportion of snake locations and random locations occurring within three meters of edge habitat.

Microhabitat use was examined by comparing microhabitat characteristics at snake locations to random locations. I used bivariate correlation to remove correlated variables and determined which remaining variables best predicted of Northern Copperhead habitat use through the use of multivariate logistic regression (backward Wald). While paired logistic regression would be better suited to this type of analysis, a low sample size at Clark State Forest prevented its use for this population. Therefore, I opted to use the backward Wald procedure for the Clifty Falls State Park population as well to facilitate a more direct comparison of the two populations.

Results

Radiotelemetry

In total, I captured and monitored 22 Northern Copperheads at Clifty Falls State Park and 9 Northern Copperheads at Clark State Forest. Microhabitat and macrohabitat analyses for Clark State Forest were based on data collected on 9 Northern Copperheads during the 2009 field season. For Clifty Falls State Park, macrohabitat selection analyses utilized data from all four years of the study (2008-2011), whereas microhabitat analyses utilized data from 2008 and 2009 since data collection on several of the variables was discontinued in order to investigate additional aspects of habitat use during the 2010 and 2011 field seasons.

General Observations

Breeding and Parturition

All observations of courtship and copulation occurred during late summer and fall, with a peak in late September and early October (range: August 17 – November 7). Of 17 observations of parturition (including 6 untracked snakes), nine took place in rock crevices (Clifty Falls State Park), seven occurred in hollow logs (Clark State Forest), and one took place in a brush pile (Clifty Falls State Park). Of these events, 11 occurred in late August while the rest occurred in September. The furthest distance of a birthing site from a hibernaculum was 187 meters, and the closest was 23 meters (each at Clifty Falls State Park). Rookeries (aggregations of gravid females) were common at both study sites. At Clifty Falls State Park, two rookeries consisted of man-made rock foundations, while two additional sites occurred in rocky outcroppings. At Clark, two rookeries consisted of fallen timber, which had decayed and hollowed. Rookeries at both study sites were each situated on south to south-west sloping ridges with open canopy. Aggregations of at least 11 gravid females were observed at Clark, and aggregations of gravid females at Clifty Falls State Park typically consisted of between three and five individuals at any given site.

Post-partum females were observed to remain at their birthing sites for a range of two – seven days following parturition before dispersing to habitats more typical of nongravid female summer foraging sites (*i.e.*, forest gaps with fallen timber or brush piles). I observed seven successful foraging events by post-partum females, each within two weeks of parturition, and most females appeared to feed following parturition (evident from bulges).

Hibernation

Post-partum females typically returned to hibernacula by the end of September, shortly after foraging. Nongravid females typically returned to hibernacula between late-September and mid-October, and approximate dates of return to hibernacula by males ranged from October 15 – November 27. Movement during late November with air temperatures below 20 °C was not uncommon for males, which appeared to undertake extended migrations in the fall while mate-searching. For example, a large adult male at Clifty Falls State Park was observed on the surface on November 26, 2010 near the top of an exposed hillside powerline cut situated approximately 200 meters from its previous year's hibernaculum. It had been observed courting a radiotagged female in this area two weeks prior. It spent the majority of the winter inside a manhole until moving approximately 200 meters during icy weather to its hibernaculum where it was observed at the surface again on February 24, 2011 during a light rain with air temperatures around 3 °C. This was the coolest period of surface activity recorded for any copperhead at either study site.

Hibernacula at each study site were situated on south-east or south-west facing slopes where overstory canopy cover ranged from 70-100% during summer months.

However, these sites were relatively exposed during winter months. Also common among all sites was the presence of semi-dry hillside streams or seeps, which maintained moisture without freezing throughout the winter.

Seasonal Habitat Use

Dispersal from hibernacula typically occurred during the last two weeks of April, when snakes at each study site selected transitional habitats on slopes near the tops of ridges. These sites were always positioned between hibernacula and summer foraging or gestation sites. Copperheads at Clifty Falls State Park appeared to increase their use of leaf litter and logs during this period and were less often visible above leaf litter compared to other times of the year. Unlike the Clark State Forest population, however, they were found under decaying logs rather than within them. Preference for leafy substrates appeared to decrease for males and gravid females during the summer when all males utilized grassy substrates, and gravid females selected rocky substrates. Nongravid females continued to exhibit preference for logs and fallen timber throughout the year, presumably as foraging sites. At Clark State Forest, there did not appear to be an obvious distinction between habitats selected by males and nongravid females, whereas gravid females were always located inside a log or within one meter from a hollow log.

With the exception of males during the breeding season, snakes that were tracked multiple years at Clifty Falls State Park rarely (if ever) altered their movement patterns, exhibited high site fidelity, and used a limited number of foraging and gestation sites within and between years. Younger snakes did appear to exhibit some ‘exploring’ behavior. A subadult male (when captured) that was tracked for three years made several sporadic movements to different habitat patches throughout the first year that it was radiotracked but settled into a pattern by the second year that included several sites it visited the previous year. It visited only one new site during its third year, where it mated in the fall. Similarly, a subadult female (when captured) that was tracked for three years made several sporadic movements the first year, but again settled into a pattern by the second year that included only sites that it visited the first year. In its third year, it moved sporadically again but by mid-July moved to the ‘overlook’ where it gave birth that fall. This was the furthest into an activity season that any gravid female made multiple long-distance movements (over 50 meters).

Foraging

Overall, copperheads at each study site exhibited primarily nocturnal patterns of foraging and long-distance movement during warmer months and were more crepuscular during spring and fall. Nocturnal movement appeared rare below 21 °C and most common when night temperatures exceeded 25 °C.

Individuals in each population were observed foraging on small mammals (in order of prevalence: *Peromyscus, Microtus, Tamias,* and *Scalopus*), cicadas (Family: Cicadidae), and several unidentified invertebrates. At Clifty Falls State Park, males spent summer months in grassy or other early successional habitats (*e.g.*, grassy perimeters), whereas nongravid females selected forest gaps containing fallen timber or manmade bush-piles. All gravid females at Clifty Falls State Park selected glades or glade-like habitats having intense sun exposure and low levels of vegetation. They were never observed foraging or exhibiting any sign of having recently foraged (bulges).

Macrohabitat Selection

Clark State Forest

The activity ranges for all Northern Copperheads at Clark State Forest were less than five hectares (ha) in total area (mean = 3.69 ha, minimum = 2.37 ha, maximum = 4.81 ha). Nonrandom macrohabitat selection was detected at the landscape level (overall: $\chi^2 = 7.98$, df = 2, $P = 0.019$) where forest was preferred over field ($t_7 = 2.517$, $P = 0.040$) and other ($t_7 = 2.519$, $P = 0.040$). There was no significant difference in macrohabitat selection when considering field compared to other ($t_7 = 0.39$, $P = 0.708$). At the activity range level, field was combined with other due to the lack of availability within the activity ranges, but Bycomp did not detect any nonrandom selection of macrohabitat when considering forest and field/other ($\chi^2 = 1.34$, df = 1, $P = 0.247$).

Clifty Falls State Park

The activity ranges of snakes at Clifty Falls State Park ranged between 0.01 and 29.45 hectares. Average home range size for males was 16.49 (minimum = 6.09, maximum = 29.45 ha), and average home range size for females was 1.83 (minimum = 0.01 ha, maximum = 5.49). This difference was significant ($t_8 = 5.05$, $P < 0.001$). When comparing the same females between gravid and nongravid years, gravid females had a smaller home range with fewer long-distance movements (t_2 = -4.44, P = 0.047).

Compositional analysis revealed significant differences in habitat preference for the Clifty Falls State Park population at both the landscape (λ = 0.01, F_{24} = 813.96, $P <$ 0.001) and activity range (λ = 0.467, F_{24} = 9.12, $P < 0.001$) level. At the landscape level, Glade was the most preferred habitat, preferred significantly over Field (t_{26} = 5.27, $P <$ 0.001). Field was in turn preferred significantly over Forest (t_{26} = 3.9674, $P < 0.001$), and Forest was preferred significantly over 'Other' (t_{26} = 11.56, $P < 0.001$). Selection vectors were positive for Glade (0.46 ± SE 0.06) and Field (0.09 ± SE 0.03) and negative for Forest (-0.35 ± SE 0.05) and 'Other' (-0.18 ± SE 0.00). At the activity range level, Glade was preferred over both Forest (t_{26} = 3.478, P = 0.003) and 'Other' (t_{26} = 4.709, P = 0.001), but there was no significant difference between Glade and Field (t_{26} = 0.820, P = 0.474). Field was also preferred significantly over Forest (t_{26} = 2.470, P = 0.027) and 'Other" (t_{26} = 4.415, P = 0.001), and Forest was preferred significantly over 'Other' (t_{26} = 2.406, P = 0.020). Selection vectors were positive for Glade (0.30 ± SE 0.05) and Field (0.09 ± SE 0.02) and negative for Forest (-0.36 ± SE 0.04) and 'Other' (-0.02 ± SE 0.01).

Compositional analysis including different forest types indicated significant differences in habitat preference. With forest divided into three types (*i.e.*, dry-upland, dry-mesic upland, and mesic upland), compositional analysis ranked habitats as follows in order of decreasing preference at the landscape level: Glade >>> Dry Upland (t_{26} = 3.957, P = 0.001) >>> Grassland (t_{26} = 3.957, P = 0.001) > Talus (t_{26} = 1.494, P = 0.156) > Dry-Mesic (t_{26} = 1.742, P = 0.081) > Mesic (t_{26} = 1.742, P = 0.081) >>> Anthropogenic (t_{26} = 3.902, P = 0.001, with ">>>" indicating a significant difference (*t* statistic and *p*-values in parenthesis correspond to the relationship between the two preceding habitats based on randomization simulations). Overall, selection vectors were positive for glade (0.44 ± SE 0.06), dry-upland (0.15 ± SE 0.04), grassland (0.08 ± SE 0.03), and talus (0.02 ± SE 0.01) and negative for dry-mesic upland (-0.32 ± SE 0.02), mesic upland (-0.20 ± SE 0.13) and anthropogenic (-0.20 ± SE 0.0) (Fig. 1). Compositional analysis ranked habitats similarly at the activity range level: Glade>Grassland>Dry Upland> Talus>Anthropogenic>Dry-Mesic>Mesic, although there were fewer significant differences. Glade was preferred significantly over all habitats except Grassland (t_{26} = 1.083, P = 0.323). Selection vectors were positive for Glade (0.30 ± SE 0.05) and Grassland (0.09 ± SE 0.02) and negative for Talus (-0.01 ± SE 0.01), Anthropogenic (-

0.02 ± SE 0.01), Dry Upland (-0.06 ± SE 0.05), Mesic Upland (-0.11 ± SE 0.023), and Dry-Mesic Upland (-0.19 ± SE 0.03) (Fig. 2).

Use of Edge Habitat

41.4% of copperhead locations at Clifty Falls State Park occurred directly on edge habitat compared to only 9.0% of random locations. This relationship was significant (χ^2 = 25.627, P < 0.001). Of those snake locations that occurred on edge habitat, 94.3% occurred adjacent to recreational or other human-use sites. At Clark State Forest, only 7.0% copperhead locations occurred on edge habitat compared to 7.5% of random locations.

Microhabitat Selection

Clark State Forest

The final model predicting microhabitat selection by the Clark State Forest Population contained leaf litter depth, canopy cover, and distance to native shrub and correctly predicted 83 percent of locations. Copperheads at Clark State Forest were more likely to select microhabitats in areas with greater leaf litter depth (Wald = 58.43, odds ratio = -0.371 ± SE 0.049, df = 1, *P* < 0.001), lower canopy closure (Wald = 35.46, odds ratio = 0.041 ± SE 0.007, df = 1, *P* < 0.001) and in closer proximity to native shrubs (Wald = 5.47, odds ratio = 0.334 ± SE 1.43, df = 1, *P* = 0.019) than other available microhabitats within a 20 meter radius.

Clifty Falls State Park

The final model predicting microhabitat selection by the Clifty Falls State Park population contained canopy cover, distance to overstory tree, distance to understory tree, distance to shrub, distance to rock, distance to leaf litter, and leaf litter depth. This model correctly predicted 78 percent of locations. The Clifty Falls State Park population was more likely to select microhabitats with lower canopy closure (Wald = 94.98, odds ratio = 0.0370 ± .004, df = 1, *P* < 0.001), further from overstory (Wald = 18.17, odds ratio = -0.115 ± SE 0.036, df = 1, *P* < 0.001) and understory trees (Wald = 6.28, odds ratio = -0.090 ± SE 0.036, df = 1, *P* = 0.12), in closer proximity to shrubs (Wald = 16.44, *B* = 0.17 ± SE 0.017, df = 1, *P* < 0.001), rock (Wald = 13.96, odds ratio = 0.72 ± SE 0.019, df = 1,

$P < 0.001$), and leaf litter (Wald = 13.59, odds ratio = 0.184 ± SE 0.050, df = 1, $P < 0.001$), and with greater leaf litter depth (Wald = -0.104 ± SE 0.283, odds ratio = -0.104, df = 1, $P < 0.001$) than other available microhabitats within a 20 meter radius.

Discussion

General Observations

My observations of primarily nocturnal activity patterns by copperheads during warmer months and crepuscular activity patterns during spring and fall are consistent with general perceptions of this species in Indiana and across its range (Minton, 2001; Conant and Collins, 1998). A strictly fall breeding pattern, however, is in contrast with the general view of this species, which suggests breeding behavior during both spring and fall (Conant and Collins, 1998; Minton, 2001) but agrees well with Smith *et al.* (2009) who observed 4.8% of breeding events in July, 35.7% in August, and 59.5% in September. Smith *et al.* (2009) focused on copperheads in Connecticut at the northern extent of the species' range, where a slightly shifted pattern may be expected compared to Indiana based on cooler operative temperatures (Stearns, 1992; Smith *et al*., 2009).

Due to time constraints and the nature of data collection, I was unable to obtain exact dates for emergence and return to hibernacula for any snake. This was further complicated by the fact that copperheads at each study site were observed at the surface during all months of the year except during January (although observations were biased against January due to limited time in the field). With the exception of limited basking behavior at hibernacula, surface activity between December and February was highly unusual at both study sites and has not been recorded for any pit-viper in the Midwest. Interestingly, the observation of surface activity during February was for a large adult male hibernating in an area in which common privet (*Ligustrum* sp.) had recently formed a monoculture covering the hibernaculum and surrounding area. Although purely observational in nature, there appeared to be trend for copperheads to exhibit increased basking behavior during winter months when exotic plant monocultures occurred over hibernacula. This may be a result of exotic plants lowering operative environmental temperatures at hibernacula by limiting solar radiation, but further investigation is necessary. (See Chapter Two for a more thorough discussion and some supporting data.)

While gravid females were not observed foraging or showing any sign of having recently foraged, their general behavior (remaining just visible in crevices or logs) along with their generally stouter appearance (from gravidity) may have deemed it difficult to accurately assess whether foraging actually took place. A lack of feeding behavior by gravid individuals of some snake species may be expected, although feeding by other pit-vipers (*e.g.*, Timber Rattlesnakes, *Crotalus horridus*) while gravid is known to occur (Gregory *et al.*, 1999). Moreover, gravid copperheads willingly take prey in captivity when offered (Carter, personal observations; Richard Davis, personal communication). If feeding by gravid copperheads during gestation is necessary for energy requirements, the sites they select may be important for reasons beyond thermoregulation given that they were not observed to move away from their gestation sites until giving birth. The use of hollow logs by gravid copperheads at Clark State Forest may allow these snakes to forage opportunistically on rodents and large invertebrates, whereas the use of rocky outcrops by gravid copperheads at Clifty Falls State Park probably does not afford them comparative foraging opportunities based on the known habitat preference of copperhead prey species (Getz, 1961; Kaufman and Fleharty, 1974; Barnum *et al*., 1992).

Macrohabitat Selection

While Northern Copperheads at each study site appeared to utilize macrohabitats in a unique way, this difference appears to be the result of different forest types, possibly owing to the inherently different levels of sunlight penetration and moisture that affect copperheads directly or indirectly through foraging opportunities or other unknown/unmeasured factors. Given a strong preference for open canopy habitats such as glades, dry-upland (sparse oak-hickory forest), and grasslands (open fields), copperheads at each study site appear to be limited in habitat utilization by factors related to thermoregulation. This may be especially true for gravid females at Clifty Falls State Park, which exhibited a higher degree of preference for glade habitats than either males or nongravid females (Fig. 1). Preference for grassland, however, seems to be driven by males, with very low selection by females and even a low degree of avoidance by gravid females (Figs. 1 & 2). Overall, preference for grassland by males, glades by gravid females, and forest gaps—containing fallen timber or brush piles—by nongravid females appears to be the general rule for copperheads at Clifty

Falls State Park. Gravid female habitat selection is probably driven more by thermoregulatory constraints, whereas males and nongravid females spend the summer activity season foraging (Chapter Two). Convergence of habitat use by males and nongravid females typically occurs beginning in late August or September when males undertake relatively straight-line migrations to female summer habitats. Due to low a sample size at Clark State Forest, I was not able to explore sex-specific patterns in habitat use by this population. However, general observations indicate that gravid females preferentially select exposed ridge-tops with a southern or western exposure. The only snake utilizing grassland at Clark was a male, which was the only snake with grassland occurring within its home range.

All copperheads at Clark State Forest had relatively small home ranges compared to the Clifty Falls State Park population and to the results of previous studies (*e.g.*, Reinert, 1984; Smith *et. al.* 2009). This may be explained by the more homogenous dry-upland landscape present at Clark State Forest. The more heterogeneous canyon landscape at Clifty Falls State Park and most other copperhead habitats creates a habitat mosaic with greater distance between habitats. This may also explain the lower minimum home range size of copperheads at Clifty Falls State Park, where the fitness costs related to travelling to spatially isolated, more distant, habitats may be too great—potentially forcing younger snakes and gravid individuals to settle for lower quality habitat in closer proximity to hibernacula.

Interestingly, Smith *et al.* (2009) found that copperheads at the northern extent of their range “used primarily upper-elevation grassy glades.” This probably would not differ for Clifty Falls State Park or Clark State Forest if grassy glades were more abundant at either site. However, it appears that grassy glades are substituted for grasslands or forest gaps. While copperheads at Clifty Falls State Park do exhibit preference for glades, these glades are mostly remnant in nature and lack native herbaceous growth. Clark State Forest lacks glades altogether and has an extremely low availability of grassland while the majority of forest is dry-upland forest with thinner canopy than is present at Clifty Falls State Park. This is a product of the physiographic region wherein Clark State Forest lies (*i.e.*, Knobstone Escarpment section of the Norman Upland). This region is characterized by higher elevation ridges composed primarily of dry oak-hickory upland. Clifty Falls State Park on the other hand lies within the Muscatatuck Plateau, an area of lower elevation beech-maple forest (Homoya, 1985).

Microhabitat Selection

While most Northern Copperheads are found in habitats composed of high amounts of rocky substrates, talus, and/or rocky outcroppings such as that seen at Clifty Falls State Park (Minton 2001; Reinert 1984; Smith *et. al.,* 2009), Clark State Forest contains very little surface rock in comparison, and the final microhabitat model did not predict rock as an important microhabitat component. The Clifty Falls State Park population exhibited use of rocky substrates more typical for this species. The results concerning increased leaf litter depth as an important microhabitat component for each population are consistent with other studies of the Northern Copperhead (Fitch, 1960; Smith et al. 2009) as are results concerning use of lower canopy cover (Fitch 1960; Minton 2001; Reinert 1984; Smith *et al.,* 2009). Leaf litter depth is a potentially important microhabitat characteristic for both foraging/hunting, concealment, and thermoregulation. Large insects and rodents (known prey items of this species) utilize leaf litter, providing copperheads with a potential food source. Leaf litter also provides preferred ambush sites for many pit-vipers such as copperheads and Timber Rattlesnakes (*Crotalus horridus*), which benefit from a cryptic pattern ideally suited to leafy substrates (Minton 2001; Reinert, *et al.* 1984). Leaf litter may also be an important microhabitat component for thermoregulation, allowing snakes to move vertically within the leaf litter column as leaf litter beds maintain more stable temperatures and retain higher levels of moisture than the surface, potentially allowing snakes to maintain body temperatures closer to their preferred range with little energy expenditure (Jaeger 1980; Magura *et al*., 2005). Copperheads at Clark State Forest were often observed moving beneath the leaf litter layer, sometimes for several meters.

Although distance to log was not significant for either population, it remains likely that the overall abundance of logs at Clark State Forest masked their importance as microhabitat components. Northern Copperheads at Clark State Forest were most often found situated within one meter or less of hollow logs (62 %), and snakes were located inside, under, or in direct contact with logs during 32.1% of all locations. Additionally, all known parturition sites and rookeries (including those of several untracked snakes) at Clark State Forest were located within hollow logs or stumps, indicating that logs may be a vital structural component for gravid females and may take the place of rock crevices as used by gravid copperheads at Clifty Falls State Park. Moreover, as ambush predators, logs provide suitable sites for pit-vipers to locate and acquire small mammals (Reinert 1984). Interestingly, copperheads at Clifty Falls State Park were never observed inside logs, and only nongravid females were observed utilizing logs or fallen timber during summer months.

A strong association with shrub cover, as exhibited by both populations, is not supported by any previous work. Instead, most have found a stronger relationship with lower densities of woody understory vegetation and increased use of native grasses (Fitch 1960; Minton 2001; Reinert 1984; Smith *et al.* 2009). At Clark State Forest, it is possible that in the absence of surface rock and herbaceous ground cover the snakes have locally adapted to utilize shrubby cover as refuge sites. However, native shrub was a positive predictor of snake habitat at Clifty Falls State Park as well. Given the nature of data collection (distance measurements), shrubs may not actually be important as a microhabitat component per se but rather shrubs themselves are associated with the types of habitats that copperheads select at each site. In other words, copperheads may not be utilizing shrubs as a microhabitat component as much as they are utilizing areas where shrubs are a byproduct. This is probable given that copperheads at each site were associated with decreased canopy cover, and forest gaps contain an abundance of shrub growth in the form of *Smilax and Rubus* at both Clark State Forest and Clifty Falls State Park. Nonetheless, it remains possible that shrubby forest gaps take the place of grasslands in terms of foraging given the typically high abundance of small mammals in these habitats (Wolfe and Rogers, 1969; Menzel *et al.*, 1999). The final model for Clark State Forest also indicated a more random association with herbaceous ground cover, which would be expected if this assessment is accurate. Foraging by males at Clifty Falls State Park was most prominent in early successional fields, and foraging by females was prominent in shrubby forest gaps. The lack of herbaceous ground cover as a significant parameter in the final microhabitat model for Clifty Falls State Park is probably due to avoidance by gravid females (Figs. 1 & 2).

Canopy gaps are important for many forest reptiles, including pit-vipers such as the Timber Rattlesnake (*Crotalus horridus*) and Eastern Massasauga (*Sistrurus catenatus catenatus*) (Reinert 1984; Marshall *et al*., 2006; Harvey and Weatherhead, 2010). Gaps not only provide potentially abundant food sources (as mentioned previously) but are also necessary for efficient thermoregulation among most temperate forest reptiles (Lillywhite and Henderson, 1993; Vitt *et al*., 1998; Greenberg, 2001). At Clark State Forest, timber harvest along ridge tops appears to benefit copperheads by increasing both the amount of canopy openings in the forest interior as well as the number of logs and cut stumps that appeared to be artifacts of harvest. Several studies have investigated the impacts of timber harvest on wildlife, with many variable conclusions (see: Gardner et al. 2007). Records of timber harvest were not made available for Clark State Forest, thus I was not able to quantify an association between copperheads and harvested areas. Qualitatively, snakes appeared to exhibit preference for harvested ridges as evidenced by aging heavy equipment paths and remaining cut stumps and non-select logs on the large majority of ridges utilized by snakes. Whether this superficial association is due to timber harvest or habitat conditions preceding harvest is unknown. Interestingly, the Clifty Falls State Park population also exhibited a strong association to human-disturbed habitats. While logging does not occur at Clifty Falls State Park, snakes utilized the edges of hiking trails and recreational sites as well as managed habitats (*i.e.*, exotic vegetation control) and the remnants of hand-laid stone foundations.

Conclusions

Overall, copperheads at each site rely on increased leaf litter depth, native shrubs, and canopy gaps in a forested landscape. The key differences in habitat use appear to be the result of habitat availability rather than a true separation in behavior and resource selection patterns. Clark State Forest lacks abundant surface rock, glades, and grassland but snakes appear to compensate by utilizing hollow logs, stratified leaf litter, and canopy gaps with shrubby cover. This compensation does not appear to carry any costs for snakes since the seemingly healthier population also appears to expend far less energy in acquiring and utilizing resources in the overall higher quality and more homogenous landscape. This is partially evidenced by the smaller home range sizes of copperheads at Clark State Forest compared to Clifty Falls State Park as well as over seven years of visual monitoring that indicates an exceedingly higher population density for Clark State Forest than for Clifty Falls State Park (Carter, Hoffman, and Eads, personal observations; Richard Davis—Indiana DNR, personal communications).

While copperheads at Clifty Falls State Park appeared to avoid forest, a more in-depth investigation into the use of different forest types confirmed that the primary differentiation in habitat use between the two populations was not as significant as would have been thought if basing results only on simpler macrohabitat delineations (*i.e.*, a single category representing forest). Moreover, while I was unable to analyze sex-specific habitat use at Clark State Forest (due to low sample size), the results for Clifty Falls State Park indicate that habitat use can differ significantly between sexes and reproductive groups, not simply between gravid and nongravid individuals as is often true among snakes (*e.g.*, Charland and Gregory, 1995; Gregory *et al*., 1999).

Management Implications

Resource managers often base management decisions on data obtained from wildlife populations that are distinct from the population(s) they are attempting to manage. This type of scenario can lead to management decisions that fail to address important wildlife resource selection parameters given that many populations exhibit distinct habitat use patterns based on a number of historical factors related to history of colonization (*e.g.*, dispersal and adaptation to evolutionarily novel habitats as well as genetic drift) (Witte *et al*., 1990; Turingan *et al*., 1995; Trussell, 1997; Mittelbach *et al*., 1999). A related aspect of many species management plans is that they typically entail management of habitat in a specified direction that is deemed appropriate for a particular species. These efforts carry the risk of failing to conserve biodiversity in important ways. If protection of a critically imperiled species is the goal, these efforts can fail in the manner specified above in which differences in habitat utilization between populations may exist, and low genetic variation coupled with low phenotypic plasticity have the potential to prevent a population from utilizing managed habitat if that habitat was not used preferentially by a population before management began. Secondly, if management is more preemptive in nature, and populations are not at immediate risk of extirpation, management may be viewed as preventing adaptation and limiting genetic diversity by favoring individuals that fit the model habitat plan. While these views have not been tested empirically in the presently stated manner, a great deal of support exists from the field of evolution and ecological genetics (see Schluter, 2001).

The results of this study thus emphasize the importance examining both sex-specific and multi-scale habitat use patterns when developing management guidelines.

If based a simple macrohabitat classifications and pooled populations, potentially critical habitat may have been overlooked for declining copperhead populations in southern Indiana. By and large, the Clifty Falls State Park population will benefit from restoration and/or maintenance of glades, grasslands, and dry-upland forest while the Clark State Forest population appears stable. Passive management at Clark State Forest might entail maintaining thin canopy dry-upland forest. However, current timber harvest practices seem to be adequate in maintaining and/or creating preferred habitat for this population.

Clifty Falls State Park is also heavily burdened by the introduction and proliferation of exotic invasive plants. The vast majority of habitat available to copperheads within the park is composed of exotic plant monocultures (Chapter Two). A strong association to edge habitat by copperheads at Clifty Falls State Park (but not at Clark State Forest) may be related to the higher availability of dense canopy forest relative to more open natural habitats, but it seems equally probable that high densities of exotic plants within the forest interior are ‘pushing’ snakes into edge habitats and into closer proximity to humans, providing some support for the benefits of managing canopy gaps in the forest interior.

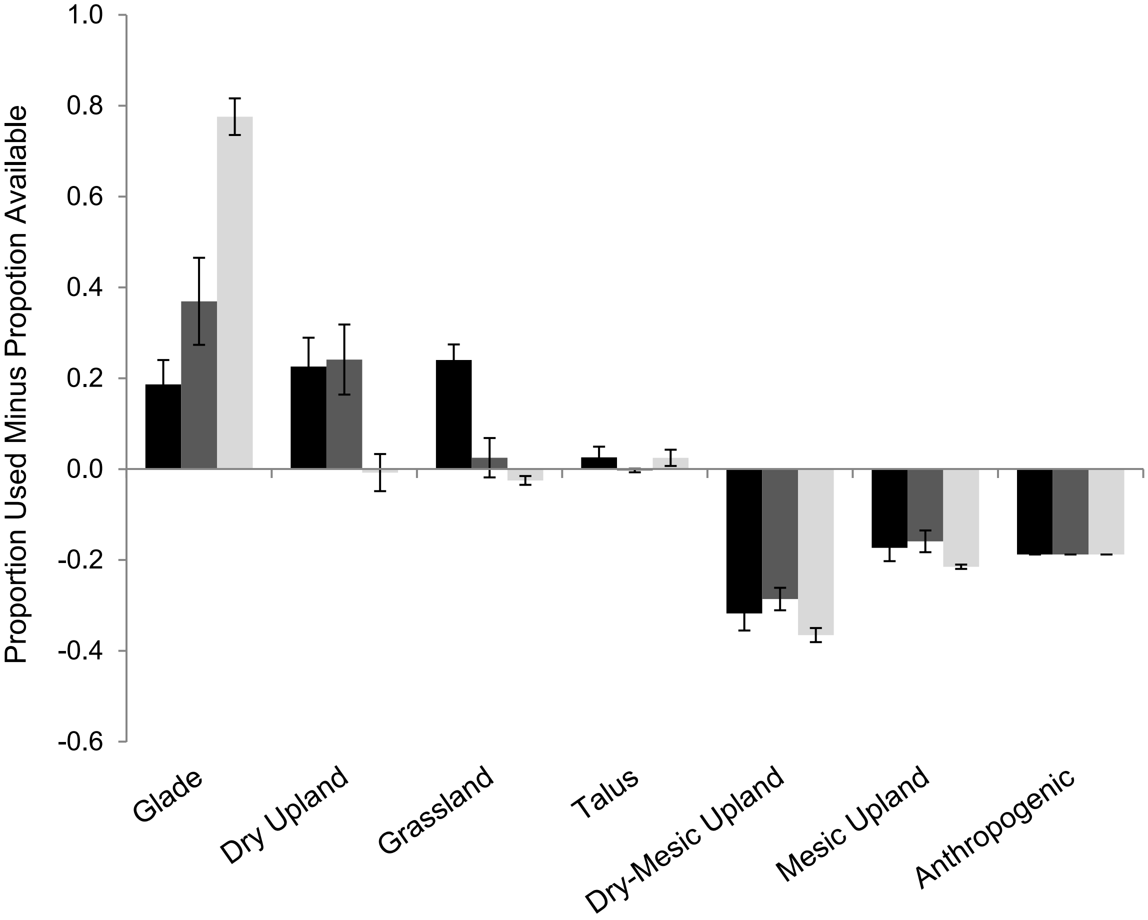

Figure 1.1. Proportion of used habitat minus proportion of available habitat at the landscape level for male (black bars), nongravid female (dark gray bars), and gravid female (light bars) Northern Copperheads at Clifty Falls State Park. Error bars represent two standard errors above and below the mean.

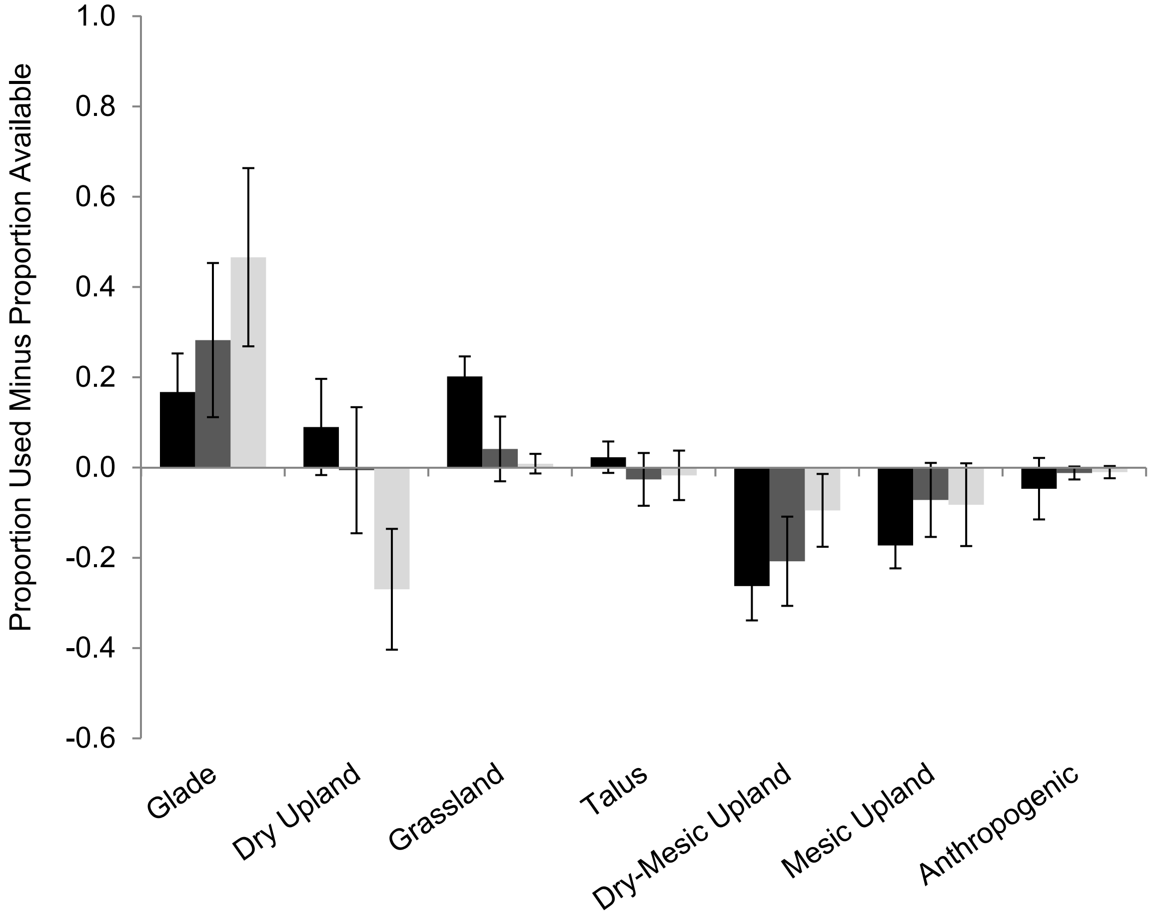

Figure 1.2. Proportion of used habitat minus proportion of available habitat at the activity range level for male (black bars), nongravid female (dark gray bars), and gravid female (light bars) Northern Copperheads at Clifty Falls State Park. Error bars represent two standard errors above and below the mean.

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CHAPTER TWO

IMPACTS OF INVASIVE PLANTS ON NORTHERN COPPERHEADS

Introduction

Invasive species are known to alter landscape structure and function, often impacting native wildlife in the process. They are thought to be a leading factor in the decline of approximately 42% of species protected by the Endangered Species Act (Pimental *et al*., 2005), and calculations completed in 2005 utilizing the IUCN Red List database suggest that of the 170 extinct animal species for which causes are known, 91 (54%) are at least partially attributable to invasive species (Clavero *et al*., 2005). While invasive species are known to have severe ecological impacts, the specific effects that these invaders have on particular wildlife are not well understood. Indeed, many scientists have called for action on invasive species, insisting it is a matter of great urgency and demanding executive and congressional action (Union of Concerned Scientists, 2004). At the same time, however, policy makers have expressed that they are in desperate need of tangible evidence identifying the effects of invasive species before they can make important decisions regarding the issue (CABI, 2008).

The impacts of invasive plants on wildlife can be difficult to quantify, and few researchers have attempted to do so (Levine *et al*., 2003; Pysek *et al*., 2008). While several studies have utilized changes in abundance, distribution, or health of populations as measures of the effects of invasive plants (*e.g.*, Trammel and Butler, 1995; Thompson, 1996; Benedict and Hepp, 2000; Pearson and Fletcher, 2008), such studies are mostly correlative in nature and offer little evidence of the mechanisms involved—effectively limiting their use in targeted conservations efforts. Additional studies have found certain exotic plants to be of lower nutritional value or less palatable to some wildlife (*e.g.*, Trammel and Butler, 1995; Nagy *et al*., 1998; DiTomaso, 2000), but it is neither known how or if survival and fitness of these species are affected. Schmidt and

Whelan (1999) provide the only published study documenting mechanistic, although indirect, effects of invasive plants on wildlife. Their findings demonstrate that songbird nests constructed in the invasive shrubs *Lonicera maackii* and *Rhamnus cathartica* experience higher predation than nests in comparable native shrubs.

Potential Impacts of Invasive Plants on Herpetofauna

Herpetofauna are among the most vulnerable groups of wildlife (IUCN, 2010), and conservation efforts for this collective group have increased noticeably over the past decade. Nonetheless, there exists very little quantitative evidence concerning the impacts of invasive plants on herpetofauna, and Moore and Gillingham (2006) appear to provide the only published study of such potential effects. They demonstrated that the imperiled Eastern Massasauga, *Sistrurus catenatus catenatus*, avoided monocultures of exotic shrubs such as glossy buckthorn, *R. frangula*, and suggested that the mechanism behind avoidance lies in limitations on thermal opportunities imposed by these species. The Eastern Massasauga is listed as threatened or endangered across its range and is currently a candidate for federal listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 1999). Thus, their study represents a case where invasive plants may pose a direct threat to an especially vulnerable herpetofaunal (and ectothermic) species, further suggesting a need to assess the impacts of invasive plants on herpetofauna.

While the effect proposed by Moore and Gillingham (2006) of invasive shrubs on the thermal opportunities available to the Eastern Massasauga remains anecdotal, it may be an accurate assessment. A defining characteristic of many invasive plant species is the ability to drastically alter landscapes, often by forming dense monocultures where they have been introduced and have few native counterparts capable of out-competing (Richardson *et al.*, 2000). Moreover, vegetation typically influences the environmental temperatures in a given habitat both on a regional and local scale (Lim *et al.*, 2008). We might, therefore, expect that invasive vegetation has the ability to drastically alter the thermal properties of a habitat (Schmitz *et al.*, 1993), thereby greatly affecting thermal opportunities and the extent to which ectotherms can exploit those opportunities. Finally, as all physiological processes are temperature-dependent, environmental temperature is widely held as one of the primary limiting factors influencing the behavior and distribution of herpetofauna and other ectothermic organisms (Reinert, 1993). Since body temperature can also be directly linked to multiple measures of ectotherm fitness (see: Rand, 1964; Christian and Tracy, 1981; Hertz *et al*., 1982; Arnold and Bennet, 1984; Huey and Kingsolver, 1989; Huey and Berrigan, 2000), such thermal limitations imposed by invasive plants may indeed lead to changes in behavioural patterns and/or costs in fitness by limiting the range of attainable body temperatures in invaded habitats.

It would thus carry multiple implications for conservation to demonstrate the effects of invasive plants on herpetofauna, a rapidly declining group of wildlife (Houlahan *et al*., 2000; Gibbons *et al*., 2000;). By utilizing a herpetofaunal species as a surrogate species for the effects of invasive plants, we may investigate a broader range of impacts on wildlife, addressing both general ecological effects as well as more specific effects involving potential thermoregulatory limitations. To address each of the issues outlined above, I investigated the effects invasive plants the Northern Copperhead, *Agkistrodon contortrix.*

Studies of this species' ecology in southern Indiana along with reliable reports by park naturalists have identified invasive plants as a potential factor in recent localized declines (Carter and Eads, unpublished data; Richard Davis – Indiana Department of Natural Resources, personal communications). These studies have also revealed that Copperheads in southern Indiana spend the majority of the day basking or in retreat sites, showing very high fidelity to a limited number of particular sites throughout the season. Moreover, the Copperhead remains crepuscular throughout the spring and fall, switching to a nocturnal state during summer, very rarely moving from basking-retreat-site interfaces during daylight hours (*e.g.* the edge of low vegetation near canopy gaps or rock crevices at exposed outcroppings or manmade foundations) (see Chapter One). This component of Copperhead behavior leads to the reasonable assumption that sites selected for daytime basking and refuge are of utmost importance and should provide especially meaningful data on resource selection and thermoregulation that will be pertinent to this study.

Study Objectives

The ultimate goals for this study were to (1) illustrate the impacts of invasive plants on a terrestrial ectotherm—particularly the Northern Copperhead, (2) provide a basis for future research into the mechanistic impacts of particular invasive plants species, and (3) provide a meaningful framework for herpetofaunal management in invaded landscapes.

Methods

This study took place at Clifty Falls State Park (hereafter referred to as Clifty) in southern Indiana from June 2008 – November 2011. Clifty is an approximately 570-hectare state-owned park situated in the Muscatatuck Flats and Canyons region of southern Indiana. It is characterized by limestone canyons, talus slopes, and mixed deciduous upland with public use sites and hiking trails interspersed throughout. It is bordered on the south by the Ohio River and is essentially an island of semi-natural landscape within the city of Madison, Indiana. Clifty represents an ideal setting to test the impacts of invasive plants as it currently contains at least 22 of 60 invasive plant species identified as the "most unwanted" invasive plants in the state of Indiana (CAPS, 2009), facilitating investigation into the potential impacts of multiple key invasive plant species.

I captured copperheads primarily by active search and opportunistic captures in the spring of each year. Adults copperheads were outfitted with temperature-sensitive radiotransmitters (Holohil Systems, model SB-2T) and monitored by telemetry up to four times per week. Radiotransmitter implantation followed modified surgical procedures adapted from Reinert and Cundall (1982) using isoflurane as an anesthetic. I did not conduct any surgeries after September 15 of any year in order to reduce the risk of snake mortality associated with late-season transmitter implantations (Rudolph *et al*., 1998). Following surgery, snakes were housed separately in clean enclosures for a recovery period of two to seven days before being released at their original capture site. While housed, snakes were provided a hide box, heat source, and water *ad libitum* and maintained on a lighting cycle that approximated the current natural conditions at that time.

Influence of Invasive Plants on Resource Selection

Fine-grained and Intermediate Scale Habitat Selection

I recorded vegetation characteristics at snake-selected and paired random plots (control sites representing availability of habitat components). Random sites were situated within twenty meters from a snake location in a random direction and were recorded for each snake during every tracking event, giving an equivalent number of snake locations and random sites for comparison. For comparisons at the microhabitat scale, I recorded percent ground cover and modal height of native and exotic plants within a 1-meter diameter plot centered at each snake location and random site. All species of exotic plants within plots were recorded, and the dominant species of each group (*e.g.*, shrub, vine, herbaceous, and tree) was noted. For comparisons at the intermediate, or coarse-grained, habitat selection scale, I measured percent canopy closure using a spherical densitometer as well as distance to the nearest native and exotic shrub, herbaceous ground cover (*e.g.*, weeds, grasses, and forbs), vine, overstory tree, defined as ≥ 7.5 cm diameter at breast height (dbh), and understory tree (<7.5 cm dbh) (Tables A.1 & A.2). Exotic species were identified and noted in each case. I identified exotic plants using the USDA Plants Database (USDA NRCS, 2011).

Macrohabitat Preference

For comparisons at the macrohabitat scale, I first mapped exotic species in the field by recording the level of exotic plant invasion within a 30-meter radius at GIS-generated ‘random’ grid points spaced 60 meters apart. I generated 550 points within a 40-meter buffered polygon situated around the known study site, which did not change from 2009 to 2011. The level of exotic plant invasion was recorded as either pristine (exotic species absent), mostly natural (< 25% coverage of exotic species), semi-natural (25 – 50% exotic species coverage), mostly exotic (50 - 75% exotic species coverage), exotic monoculture (75 – 100% exotic coverage, single species), or as a stratified mixture of exotic species (75 – 100% exotic species coverage, stratified with multiple species). I recorded the dominant species as well as all other exotic species occurring within 30 meters of each point. The distribution of exotic plant species was also determined with a hand-mapping technique using aerial photographs at each gridded random point. Due to the gridded nature of each point, belt transects were typically employed using two individuals for visual searches of exotic plants. I digitized hand drawn maps in ArcMap by generating polygon layers representing the known boundary of each invasion level value along with species.

An assumption of the hypothesis that exotic plants impact habitat use by snakes is that exotic plants actually occur randomly or show a positive nonrandom association with respect to habitat preferred by copperheads (as opposed to copperheads simply exhibiting preference for habitat that is not readily invaded by exotic plants). To address this issue on a macrohabitat scale, I used the Spatial Analyst extension in ArcMap 10 to employ a kriging interpolation of invasion level points. This essentially bled out smaller habitat patches, introducing a higher-scale, coarser-grained, map of invasion level relative to hand-drawn maps. To provide a comparison to the coarse-grained invasion level, I explored kernel density estimators for habitat that was used by the entire copperhead population at Clifty using the Spatial Analyst extension in ArcMap. I randomly selected an equal number of locations from each individual snake to prevent bias in kernel density estimates based on number of locations. This was appropriate in comparison to generating individual kernel densities for each snake since I was concerned with broad-scale habitat in which the population as a whole was associated with rather than association with any particular snake. I began by using a search radius of 50 m^2 and gradually increased the search radius by a factor of 50 square meters until a kernel density surface was produced that encompassed 95% of all snake locations. I maintained a constant smoothing factor between iterations, which was the default set by the Spatial Analyst extension that is equal to the shortest width or height of the extent of the locations used in the analysis as measured in the output layer and then divided by 250 (ESRI, 2010). Finally, I extracted raster values from both the kriging analysis (for level of invasion) and the kernel density estimates to 2000 random points generated across the study area, which were later used to analyze the relationship between broad-scale occurrence of exotic plants and copperheads. Each random point was thus associated with a pair of values—one value representing the level of exotic plant invasion and the other value representing core copperhead habitat.

Impacts of Invasive Plants on Thermoregulation

Determining Preferred Body Temperature Range

In order to quantify the impacts of exotic plants on thermoregulation by copperheads, I first determined the range of temperatures that copperheads prefer under conditions of minimal thermoregulatory costs. ‘Preferred body temperature range’ is a theoretical estimate of the upper and lower thermoregulatory set points of a behavioral thermoregulator, which includes most ectotherms such as snakes (see Huey and Slatkin, 1976; Hertz et *al*., 1993). I use T_{pref} in place of the conventionally assigned 'T_{set}' herein to describe this index.

To determine T_{pref}, I first constructed two rectangular thermal gradients (200cm x 46cm e x 20m) from plywood using metal sheeting and copper coils as a conductive base. I lined the sides and chambers with insulation foam, and the tops were constructed from plexi-glass. Each gradient consisted of 10 paired chambers running the length of the gradient (20 chambers total). Ten chambers on one side were lighted using soft even fluorescent bulbs, and the opposite paired chambers were each covered to provide refuge. A three inch square hole passed through the lighted side of the gradient and ran the entire length of the gradient in order to provide simple passage between chambers while still maintaining insulation and uniform temperature within each chamber. A thermostat controlled heat pad was placed at one end of each gradient and chilled water (18°C) was circulated through copper coils situated under the opposite ends. Due to difficulties in obtaining a smooth temperature gradient, the top of each shaded chamber was also heated from above using individual thermostat-controlled heat pads designed for standard terrarium use. Gradients ranged from 18-40°C in order to provide a wide range of temperatures for snakes to select.

I outfitted five individual males, nongravid females, and gravid females with *external* temperature loggers (Thermonchron iButton, Model 1922L, Embedded Data Systems) and placed each snake alone in a thermal gradient that was maintained inside a laboratory environmental chamber located at Hanover University, in Hanover, Indiana. Copperheads were collected from several locations in southern Indiana in order to both minimize any impacts on the study population and to ensure an adequate sample size. Each snake was housed alone in a thermal gradient, and its body temperature was logged every 10 minutes for 48 hours (Blouin-Demers and Weatherhead, 2001). As snakes may have altered set points in body temperature during stressful conditions (Burns *et al*., 1996), all subjects were given an acclimation period of 24 hours in an attempt to reduce these potential effects before determining T_{pref}. This translated to a total of 72 hours within a thermal gradient including the acclimation period.

Determining Operative Environmental Temperatures

To determine the environmental operative temperatures (T_e) available to Copperheads at Clifty, I placed biophysical models of Copperheads containing a thermocouple (Thermonchron iButton, Model 1921G, Embedded Data Systems) in invasive plant monocultures and areas lacking invasive species. Biophysical models were constructed from copper tubing and painted to approximate the absorbance and reflectance of live copperheads (Peterson *et al.*, 1993; Shine and Kearney, 2001). A thermocouple was suspended inside each tube, the tubes were filled with water, and the ends were sealed with rubber stoppers. I validated models by comparison to both live copperheads and freshly-killed copperhead carcasses (road-killed individuals). I placed a temperature logger inside the body cavity of road-killed carcasses or used radiotelemetered snakes that were outfitted with temperature sensitive transmitters. I then placed physical copper models and snakes in similar conditions in the field for a duration of 5 – 8 hours. This was repeated using three separate snakes that spanned the body mass and length range of copperheads at Clifty (mass: 121.9 – 516.8 g, snout-vent length: 53.0 – 87.4 cm), and each snake and model were tested at high sun intensity and low sun intensity. After testing several tubing size and color configurations, I used 16 cm sections of 2.54 cm diameter thin-walled copper tubing (painted with Krylon light brown #53562).

I deployed models among defined macrohabitats (area ≥ 40 m^2) in the field, including closed canopy forest (100% canopy closure), glade (< 15% canopy closure), native shrub, native vine, and native herbaceous-dominated habitats as well as areas dominated by different invasive plant species (see Tables 2.1 & A.3). Invasive plant sites were selected based on species composition and structure in order to facilitate testing species-specific and structural effects (*i.e.*, shrub, herbaceous, and vine). Monocultures were defined as before. T_e within each habitat type was then compared to T_{pref} through multiple methods (discussed below) in order to determine the relative thermal quality of each habitat type. Ultimately, this allowed the determination of the extent to which different habitat types potentially limit thermoregulatory efficiency. Each model was moved among and within each habitat every 7-10 days throughout the 2010 and 2011 field seasons. Models were synchronized to record temperature every hour, and each 7-10 day set was matched based on slope, aspect, and—with the exception of closed-canopy forest and glade—on exposure. Models placed in non-forest and non-glade habitats were not placed in areas with greater than 15% canopy closure unless that canopy was created by the species that was being measured.

Statistical Analyses

Macrohabitat Preference

To determine macrohabitat preference, I compared the proportion of used habitats to the proportion of available habitats (using bounded polygon layer representing exotic invasion level) through multivariate analysis of variance (MANOVA) with individual snakes as the sample units (Aebischer *et al*., 1993). Since proportions of habitats sum to one and thus are not linearly independent, I utilized a log-ratio transformation to remove this independence based on the procedures of Aitchinson (1986). In the event that nonrandom habitat use was detected, I used *t*-tests to make pairwise comparisons between habitats, and a table of *randomized p*-values and *t*-statistics provided a basis for ranking each habitat in order of preference after running 999 randomization simulations using Bycomp.SAS. It is important to note that by using 999 randomization simulations, the minimum *p*-value for any pairwise comparison between habitats could be no less than 0.001 (Ott and Hovey, 1997; SAS Institute, Cary, NC). This was carried out at both the landscape level (within the range of all telemetered snakes) and home range level (within the activity range of each individual snake) (Aebischer *et al*., 1993).

To address the assumption that exotic plants occur either nonrandomly or in positive association with habitat selected by copperheads on a broader scale, I used bivariate correlation on the extracted raster values from the kriging analysis (level of invasion) and kernel density estimates (core habitat zones for copperheads).

Fine-grained and Intermediate Scale Habitat Selection

For snake-selected and paired random locations, comparisons were made utilizing conditional (paired) logistic regression (CLR). Compton *et al*. (2002) argue that CLR is a more appropriate method of analysis for paired data compared to other forms of logistic regression as it compares each snake location with its associated random point rather than pooling each category (*e.g.*, snake-selected site and random site). This ensures that microhabitat characteristics at snake locations are compared to those at random locations only when environmental conditions are similar. I calculated the difference between data values at each snake location and random location pair. This was carried out for every variable for each case, providing a matrix of predictor variables in vector format where negative values may be viewed as avoidance and positive values as preference (inverse for distance variables) (Compton *et al*., 2002). To reduce bias from individual snakes, I utilized an equivalent number of locations for each snake. Females monitored during both gravid and nongravid years were considered separate individuals. In order to reduce the high number of potential model variables, I first constructed 95% confidence intervals of each variable for each reproductive group to provide an idea of which variables deviated from a null value of zero (no selection). Variables exhibiting clear deviations from zero were then utilized in paired logistic regression analyses. In the event that two variables were highly correlated (≥ 0.50), the variable selected for inclusion in the regression model was the one for which I hypothesized would have greater biological significance for that particular case (*e.g.*, exotic shrub would take precedence over native shrub if they were found to be negatively correlated.). An intercept was excluded from each model, and the dependent variable was coded as 1 for all cases (presence value of 1 minus absence value of 0). A conditional logistic regression using typical logistic regression procedures was then used to fit snake response (of 1) to the combination of predictor habitat variables (snake locations - random locations).

I initially fit models separately for each individual snake during exploratory analyses, and several candidate models were selected based on variables that produced deviations from zero in a consistent direction across individuals of the same sex/reproductive group (Compton *et al*., 2002). Models were then fit separately for males, nongravid females, and gravid females using pooled data. Parameters were considered significant if their odds ratio confidence interval did not include 1 (Hosmer and Lemeshow, 2000). Overall model significance was evaluated using likelihood ratio tests, and I used Akaike's Information Criterion corrected for small sample size (AIC_c) to assess model weights. All models with an AIC_c score within two units of the minimum score were considered supported (Burnham and Anderson, 1998; Compton *et al*., 2002). Analyses were carried out separately at both the fine-grained (1-meter diameter plots) and intermediate habitat scale (distance variables).

Impacts of Invasive Plants on Thermoregulation

The central 50%, or interquartile range, of the temperatures selected by snakes in the laboratory thermal gradient was designated as T_{pref} (as described in Hertz *et al.*

(1993) and Blouin-Demers and Weatherhead (2001) using T_{set} in place of T_{pref}), and a separate T_{pref} was generated for males, non-gravid females, and gravid females. Differences in thermal preference between sexes (males, nongravid females, and gravid females) were tested using one-way analysis of variance (ANOVA). Analyses were carried out for the upper limits and lower limits separately. In the event differences were found, pairwise comparisons were made using Tukey's HSD (honestly significant difference) tests.

Thermal quality of each habitat type was quantified using several methods. I first used repeated measures ANOVA to determine any overall differences in thermal regimes between habitats by comparing actual T_e values matched by time, slope, aspect, and canopy shading. Multiple comparisons were determined using Tukey HSD tests. This provided a parametric measure of how different habitats measured against each other. I then calculated the proportion of operative environmental temperatures exceeding the lower bound of the preferred body temperature range. Higher quality habitats would thus exhibit a higher proportion of temperatures exceeding the lower bound (see Discussion).

Comparisons between habitats were made using a Freidman test (nonparametric repeated measures). Pairwise differences between each habitat were then determined using a Freidman post-hoc test script executed in R. This script is comparable to running multiple paired Wilcoxon signed-rank tests with a correction for multiple contrasts (Galili, 2010). Pairwise comparisons were conducted using the Freidman post-hoc test script. Finally, the conventional method of quantifying thermal quality considers operative temperatures above the upper bound of the preferred body temperature range to be equivalent in terms of thermoregulatory constraints to temperatures falling below the lower bound of the preferred body temperature range.

In following conventional methods, I used backward stepwise regression to derive equations that best predicted T_e in each habitat (Table A.4). This involved regressing temperatures recorded from physical copper models in each habitat against hourly records of air temperature or bare soil temperature, solar radiation, wind speed, and precipitation obtained from a local field data-recording weather station. I first examined the relationship between each of the independent variables to prevent multicollinearity issues. This ultimately led to testing two models for each habitat, each including solar radiation, wind speed, and precipitation and then substituting air temperature and bare soil temperature. A final model was selected for each habitat based on predictive accuracy, which was assessed using T_e records from a previous year. Equations were then used to predict T_e in each habitat under varying conditions (Blouin-Demers and Weatherhead, 2001).

I used T_e models to calculate the average deviation of operative environmental temperatures from the preferred body temperature range (denoted as d_e) for each sex/reproductive state. Temperatures within the preferred body temperature range were thus given a value of zero and deviations above and below were positive with a magnitude equivalent to the deviation from either the lower or upper bound. These values were averaged for each habitat and ranked accordingly. I repeated this process for males, nongravid females, and gravid females. I then determined whether particular sexes/reproductive states endured greater constraints by comparing mean d_e between each group (males, females, gravid females) using *t*-tests corrected for multiplicity (Bonferroni adjustments), because I predicted that gravid females would endure greater thermal constraints.

Unless otherwise noted, I used the open source statistical program R for all analyses. Analyses were considered significant at the 0.05 level, and alpha level of significance was adjusted for multiple comparisons where appropriate using Bonferroni adjustments. Means are reported in the text as ± one standard error.

Additional Mechanisms

I also conducted several exploratory analyses of additional mechanistic impacts of exotic plants. Using data collected on behavior and the level of exotic plant invasion (see *Macrohabitat Preference* above), I examined the relationship between foraging success and the level exotic plant invasion using bivariate correlation. Additionally, I regressed leaf litter depth against exotic vegetation density within one-meter random plots to determine any potential influence of exotic vegetation on leaf litter depth. This analysis used data from random locations situated within forested macrohabitats (> 50% native canopy closure), where some quantity of leaf litter should be expected.

Results

Radiotelemetry

Twenty-two Northern Copperheads, consisting of 12 females and 10 males, were tracked between June 2008 and November 2011. Four females were tracked during both gravid and nongravid years, and one snake was tracked for less than one month, providing an effective sample size of 25 snakes (8 gravid females, 8 nongravid females, and 9 males) for macrohabitat and intermediate-scale habitat preference analyses (based on differences between reproductive states as demonstrated in Chapter One). Since data was collected for densities and heights of specific exotic species within 1-meter diameter plots during 2010 and 2011 only, fine-grained habitat selection analyses included an effective sample size of 20 snakes (5 gravid females, 6 nongravid females, and 9 males).

Influence of Exotic Plants on Resource Selection

Macrohabitat Preference

At the landscape level, selection coefficient vectors (proportion used - proportion available) indicated positive selection for Mostly Natural (0.38 ± 0.05) and Semi Natural (0.11 ± 0.05) and negative selection for Mostly Exotic (-0.13 ± 0.01), Anthropogenic (-0.14 ± 0.01), and Heavy Exotic (-0.21 ± 0.03) (Fig. 2.2a). MANOVA detected a significant difference in macrohabitat preference at the landscape level ($\lambda = 0.064$, $F_{21} = 76.35$, $P < 0.0001$). Pairwise comparisons ranked macrohabitats in the following order of preference: Mostly Natural >>> Semi-Natural>>> Heavy Exotic > Mostly Exotic > Anthropogenic, with >>> indicating a significant difference. At the activity range level, selection coefficient vectors indicated a similar direction and magnitude of selection for each habitat (Mostly Natural: 0.26 ± 0.04; Semi-Natural: 0.06 ± 0.03; Anthropogenic: -0.01 ± 0.01; Mostly Exotic: -0.11 ± 0.04; Heavy Exotic: -0.19 ± 0.04) (Fig 2.2b). Pairwise comparisons ranked macrohabitats as: Mostly Natural >>> Semi-Natural >>> Anthropogenic >>> Heavy Exotic > Mostly Exotic.

On a broader scale, with finer habitat boundaries ‘bled out,’ exotic plants were more likely to occur in areas associated with the core habitat of copperheads. This relationship was significant, ($r_s = 0.60$, $P < 0.001$).

Intermediate-scale (Coarse-grained) Habitat Selection

Within the exception of exotic vine, all variables exhibited selection indices that deviated from zero for at least one sex/reproductive group at the intermediate selection scale (Fig. 2.3 – 2.5). One model for gravid females, four models for nongravid females, and two models for males were selected based on Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood ratio tests, and odds ratio significance (Table 2.2). Based on minimum AIC_c, the final model for gravid females included *canopy* + *gap* + *native shrub* + *native understory* - *exotic shrub* - *exotic herbaceous*. For nongravid females, the final model included *canopy* + *gap* + *native shrub* + *native vine* - *exotic shrub* - *exotic herbaceous*. Lastly, the final for males included *canopy* + *gap* + *native shrub* + *native vine* - *exotic shrub* - *exotic herbaceous* –*exotic overstory*. (Signs in each model indicate direction of preference.) Each variable included in the final model for each group was significant in the direction indicated based on odds ratios (Table 2.3).

Fine-grained (Microhabitat) Selection

At the microhabitat scale, all variables except *exotic tree density* exhibited selection indices with clear deviations from zero for at least one group (Fig. 2.6 – 2.8). I selected two models for gravid females, two models for nongravid females, and three models for males, each based on AIC_c, likelihood ratio tests, and odds ratio significance (Table 2.4). The final model for gravid females included *native vine height* – *native tree* – *exotic herbaceous* – *exotic shrub height* – *exotic vine height*. For nongravid females, the final model included *native vine* + *native shrub height* – *exotic herbaceous* – *exotic shrub height* – *exotic vine height*. Lastly, the final microhabitat model for males included *native shrub* + *native vine* + *native vine height* + *native herbaceous height* – *exotic herbaceous* – *exotic shrub height*. Each variable included in the final model for each group was significant based on odds ratios (Table 2.5).

Impacts of Invasive Plants on Thermoregulation

Preferred Body Temperature

One-way ANOVAs indicated a significant difference in temperatures selected in a thermal gradient between reproductive groups for both the 75% quartile (upper limits of T_{pref}) ($F_{2,15} = 4.877$, $P = 0.028$) and 25% quartile (lower limits of T_{pref}) ($F_{2,15} = 9.555$, $P =$

0.003). Post-hoc analyses (Tukey HSD test) revealed that the only difference in mean 75% quartile was between gravid females ($\bar{x}$ = 28.5, SD = 0.69) and males ($\bar{x}$ = 26.30, SD = 1.43), with nongravid female values lying near the middle ($\bar{x}$ = 27.45, SD = 1.03). For 25% quartile means, gravid females ($\bar{x}$ = 26.86, SD = 0.37) differed significantly from both nongravid females ($\bar{x}$ = 25.28, SD = 0.39) and males ($\bar{x}$ = 24.97, SD = 1.15), but no difference was found between nongravid females and males (Table 2.6).

Operative Environmental Temperatures and Thermal Quality of Habitats

Temperatures of physical copper models more closely matched the body temperature of larger snakes (350 g snake) (r_s =0.9889) than smaller snakes (200 g snake) (r_s = 0.9541). The difference in means was marginal (model mean: 34.83 ± 0.69; 350 g snakes: 35.06 ± 0.54; 200 g snakes: 34.33 ± 0.43 °C) although significant for both 200 gr snakes (t_{93} = 2.72, P = 0.004) and 350 gr snakes (t_{93} = -2.35, P = 0.021) using paired *t*-tests. However, the mean difference between physical models and either snake were within the error of the temperature loggers (Thermonchron iButton, Model 1921G, Embedded Data Systems) and between the values for both the large and small snakes. Therefore, I was confident in their accuracy and did not find the difference to be meaningful, especially given the close match to the rate of temperature change (Hertz *et al.*, 1993; Blouin-Demers and Weatherhead, 2001).

I obtained a total of 104,116 T_e measurements from 21 habitats from June 15 – November 11, 2010 and from May 1 – November 26, 2011. These included native shrub (predominantly *Rubus* spp and fragrant sumac), native vine (predominantly grape), native herbaceous (grassy fields), closed-canopy forest (surface and refuge), glade (surface and refuge), oriental bittersweet, Japanese honeysuckle, crownvetch, Japanese stiltgrass, Johnson grass, garlic mustard (1st and 2nd year), autumn olive, common privet, wine raspberry (wineberry), Armenian blackberry, jetbead, and bush honeysuckle. Garlic mustard (1st and 2nd year) monocultures were difficult to locate in open canopy habitats due to this species' shade preference. Moreover, it is often associated with moister soil habitats lacking leaf litter that do not fit general habitat use models for this population or the Clark State Forest populations (Chapter One). Therefore, while I did collect data on garlic mustard sites and display values in the figures herein, I did not include data from garlic mustard in actual thermal quality analyses with other species.

Exploratory analyses revealed no significant within-habitat differences between years, thus T_e was pooled across both years. Overall ranks based on actual T_e values placed habitats in the following order from lowest to highest mean temperature from May to November during both years: Mixed Exotics < [Refuge/Closed Canopy] < Jetbead < Autumn Olive < Oriental Bittersweet < Japanese Stiltgrass < Common Privet < Armenian Blackberry < Closed Canopy Forest < [Refuge/Glade] < Native Herbaceous < Native Vine < Native Shrub < Crownvetch < Wine Raspberry < Bush Honeysuckle < Japanese Honeysuckle < Johnson Grass < Glade. Based on weekly mean proportions exceeding the lower bounds of preferred body temperature, habitats were ranked in the following order from lowest to highest thermal quality: [Refuge/Closed Canopy] < Mixed Exotics < Oriental Bittersweet < Armenian Blackberry < Bush Honeysuckle < Japanese Stiltgrass < Autumn Olive < Wine Raspberry < Common Privet < Jetbead < Closed Canopy Forest< [Refuge/Glade] < Johnson Grass < Native Herbaceous < Native Vine < Crownvetch < Japanese Honeysuckle < Native Shrub < Glade. While the ranking values change when considering sex or reproductive state, ranking order remains unchanged.

Repeated measures ANOVA indicated a significant difference in operative environmental temperatures (T_e) between habitat types ($F_{2,79,244} = 252.35$, P < 0.001), and Tukey tests revealed multiple pairwise differences (Fig. 2.9 – 2.13). Likewise, and using males as a low end reference, Friedman tests indicated a significant difference in weekly proportions exceeding the lower bounds of T_{pref} ($\chi^2 = 88.68$, df = 24, $P < 0.001$), and Wilcoxon signed-rank tests revealed multiple between-habitat differences in the proportion of T_e exceeding the lower bounds of T_{pref}. As expected, glade habitats had the highest mean T_e (21.6 ± 0.14° C) and the highest proportion of weekly T_e exceeding the lower bounds (M = 0.270, $\bar{x} = 26.8 \pm 0.02$), whereas 'mixed exotic' habitats had the lowest mean T_e (16.2 ± 0.09° C) and the lowest proportion of weekly temperatures exceeding the lower bounds (M = 0.000, $\bar{x} = 0.026 \pm 0.011$) of all habitats measured (excluding refuge sites). From a structural perspective (*i.e.*, shrub, vine, or herbaceous), exotic shrubs (as a group) had the lowest mean T_e (17.6 ± 0.04° C) and the lowest proportion of weekly temperatures exceeding the lower bounds (M = 0.000, $\bar{x} = 0.043 \pm 0.070$). Native shrub dominated habitats had a significantly higher proportion of T_e exceeding the lower bound of T_{pref} than did any exotic shrub dominated habitat (Jetbead: $P < 0.0001$; Wineberry: $P < 0.0001$; Privet: $P < 0.001$; Autumn Olive: $P < 0.0001$; Bush

Honeysuckle: $P = 0.002$; Armenian Blackberry: $P = 0.0100$, Wilcoxon signed rank tests) (Fig. 2.9), while native vine dominated habitats had a significantly higher proportion of T_e exceeding the lower bound than did Oriental Bittersweet dominated habitats ($P = 0.003$, Wilcoxon signed rank test). However, native vine did not differ significantly from Japanese honeysuckle or crownvetch dominated habitats (Fig. 2.10). Additionally, native herbaceous dominated habitats had a significantly higher amount of T_e exceeding the lower bound of T_{pref} than did Japanese stiltgrass dominated habitats ($P = 0.024$, Wilcoxon signed rank) while neither crownvetch nor Johnson grass dominated habitats were statistically different than native herbaceous (Fig. 2.11). Finally, glade habitats were significantly greater than all but natiive herbaceous, native shrub, Crownvetch, and Johnson Grass (Figs. 2.12 & 2.13).

The conventional method of quantifying thermal quality with average deviations of T_e from T_{pref} (d_e) placed habitats in the following order of increasing quality for both males and nongravid females: [Refuge/Closed Canopy] < Mixed Exotics < Armenian Blackberry < Wineberry < Common Privet < Bush Honeysuckle < Autumn Olive < Oriental Bittersweet < Japanese Stiltgrass < Jetbead < Native Herbaceous < Johnson Grass < Native Shrub < Closed Canopy Forest < Native Vine < Japanese Honeysuckle < Crownvetch < Glade <[Refuge/Glade]. For gravid females, d_e ranked habitats as follows: [Refuge/Closed Canopy] < Mixed Exotics < Armenian Blackberry < Wineberry < Common Privet < Bush Honeysuckle < Autumn Olive < Oriental Bittersweet < Jetbead < Japanese Stiltgrass < Johnson Grass < Native Herbaceous < Closed Canopy Forest < Native Shrub < Native Vine < Japanese Honeysuckle < Crownvetch < [Refuge/Glade] < Glade (Figs. 2.14 – 2.18).

Estimates of average d_e across habitats available to copperheads indicated that Clifty Falls State Park was more thermally challenging for gravid females ($\bar{d}_e = 8.57 \pm 0.20$) than either nongravid females ($t_{21} = 5.51$, $P < 0.0001$) or males ($t_{21} = 6.49$, $P < 0.0001$). Males experienced the lowest thermal constraints as a group ($\bar{d}_e = 6.95 \pm 0.15$) but not significantly lower than nongravid females ($\bar{d}_e = 7.15 \pm 0.17$) ($t_{21} = -0.85$, $P = 0.40$). Similarly, average d_e across exotic habitats indicated that exotic plants imposed greater thermal constraints on gravid individuals than nongravid females or males (Table 2.7).

Additional Mechanisms

Observations of 49 successful foraging events by snakes were significantly negatively correlated to level of exotic plant invasion ($r_s = -1.000$, $P < 0.01$). Additionally, a regression of leaf litter depth against exotic vegetation density within one-meter random plots suggested that sites with higher exotic vegetation densities produce lower leaf litter depths, although the fit was extremely low ($r^2 = 0.040$, df = 236, $P = 0.002$).

Discussion

Northern Copperheads at Clifty Falls State Park selected habitat nonrandomly and in negative association with respect to most exotic plants at multiple spatial scales. This nonrandom association or ‘avoidance’ appears to be at least partially attributable to the low thermal quality of several exotic plant-dominated habitats. This was especially true of exotic shrubs, which had the lowest thermal quality as a group, with each exotic shrub species exhibiting only marginal differences in thermal properties between other exotic shrubs (Fig. 2.9, 2.12, 2.13, 2.16). Exotic shrubs were a negative predictor at every spatial scale for all sexes/reproductive groups. Exotic vines and exotic herbaceous did not exhibit such clear relationships between thermal quality and avoidance by copperheads. In fact, some exotic habitats were either equivalent or even higher in thermal quality than many native habitats (*i.e.*, crownvetch, Johnson grass, and Japanese honeysuckle) (Fig. 2.10, 2.11, 2.13).

Avoidance of Particular Exotic Species

While avoidance of particular species was difficult to assess given the nature of the data collected, Japanese honeysuckle appeared to be the only exotic species that was not avoided at any spatial scale by any sex or reproductive group. Conversely, oriental bittersweet, the next most abundant exotic vine at Clifty, appeared to be avoided at multiple scales, and it exhibited low thermal quality according to all measures. This may explain results concerning exotic vine density as the only model variable found to be non-significant across all groups in microhabitat selection models: selection for habitats containing Japanese honeysuckle probably masked an avoidance of bittersweet, which tends to be more habitat-specific (Japanese honeysuckle occurs in denser patches at Clifty than Japanese honeysuckle). This may also help explain a complete lack of exotic vine as a significant parameter in intermediate scale habitat selection models. One additional possibility for avoidance at this coarser-grained scale (relative to microhabitat), however, is that many exotic plants thrive in early successional habitats such as old fields, talus, and glades due to low competition with native vegetation and high levels of disturbance (Lake and Leishman, 2004). Given the dependence of copperheads on glades and other early successional habitats as well as the low abundance of these habitats at Clifty (see Chapter One), it may then be difficult for snakes to avoid some exotic plant species. Selecting microhabitats with lower heights may then be a strategy for overcoming thermal constraints. A side note to this is that copperheads were observed exhibiting arboreal behavior only in areas with tall exotic vegetation growth. This form of behavior is extremely unusual, and to my knowledge, has never been reported for copperheads. Furthermore, exotic vine height was a significant negative predictor at the fine-grained scale for gravid females and nongravid females, further supporting the idea that lower lying and more sparsely growing exotic vine species such as Japanese honeysuckle were not necessarily avoided when snakes were able to bask above the foliage layer. However, higher, denser, vines occurring on glades and in forest gaps such as oriental bittersweet (at Clifty Falls State Park) were avoided.

In each fine-grained microhabitat model, exotic vegetation height was significant for a particular structural group if density was not, with the exception of exotic vines for males. Males selected grassy fields where all exotic vines tended to occur only at low densities and, if they did occur at high density, they were typically very low in height. Pairing this with the fact that males exhibited the lowest preference for glades and forest gaps (see Chapter One, Fig. 1.1 – 1.2) where exotic vines were more abundant lends even further support to this notion. In other words, a lack of availability of exotic vines in habitats that males preferentially selected throughout the majority of the active season (*i.e.*, tall grassy fields during summer), and the fact that Japanese honeysuckle occurs in habitats selected during cooler months (*i.e.*, near ridge tops on talus) probably deemed exotic vine non-significant in the final model for males.

Exotic herbaceous was avoided across all groups at the intermediate scale. Much of this avoidance appears to be the result of garlic mustard, which was often within the range of telemetry random locations (control sites during radiotelemetry locations) but rarely recorded at snake locations. As mentioned previously, garlic mustard occurs in habitats that do not generally fit habitat use models for copperheads. Thus, I considered its potential effects to be minimal for copperheads and ‘avoidance’ to be the result of autocorrelation with other non-preferred habitat parameters. After removing garlic mustard from analyses of exotic herbaceous, the remaining three exotic herbaceous species included Johnson grass, Japanese stiltgrass, and crownvetch. Johnson grass occurred sporadically throughout the southern portion of the study site either as dense but isolated roadside or trailside patches or on glades in extremely thin and scattered clumps. Moreover, it exhibited relatively high thermal quality, which probably explains why the only exotic microhabitat variable deemed positively significant was exotic herbaceous height for gravid females. Otherwise, Johnson grass probably did not contribute significantly to additional model parameters for other groups. Given that I was interested in the structural effects of invasive plants, crownvetch was problematic in that it occurred as both vine (woody) and herbaceous, making inferences difficult. Nonetheless, this species occurred in only two sites, each of which comprised monocultures less than 40 square meters in total area—immediately adjacent to glades. This species also exhibited relatively high thermal quality. While copperheads were in close proximity to these patches, crownvetch was never recorded in any snake location plot. However, I can make no inferences on its importance given its low abundance. Finally, Japanese stiltgrass occurred in nearly all habitats selected by copperheads with the exception of glades, where it was restricted to the margins. Thus, its effects appear to be most substantial for males and nongravid females, which show preference for old fields/grassy perimeters and forest canopy gaps, respectively.

Male copperheads had the lowest preferred body temperature during gradient trials, and males of other snake species are known to thermoregulate less precisely than gravid and nongravid females (see: Blouin-Demers and Weatherhead, 2001). Moreover, male copperheads exhibited the highest variance and range in the temperatures they selected in thermal gradient trials (Table 2.6). Thus, one might expect that males would inherently demonstrate decreased avoidance of various exotic plants compared to females (of either reproductive state). However, it appears that either exotic invasive plants limit thermal opportunities to the extent that even males avoid them, or there are additional factors influencing avoidance of, or causing an indirect negative spatial relationship to, many exotic plants among male copperheads. The former is most likely at Clifty, although effects on foraging presumably exist. Most exotic shrub species occur within open fields, canopy gaps, talus slopes, and edge habitats that are preferentially selected by male (and female) copperheads (see Chapter One). As previously mentioned, this is also true for Japanese stiltgrass. Given the rapid nature of invasion and taller, denser, growth by species such as autumn olive, bush honeysuckle, and privet (reviewed in: Webster *et al*, 2006), it is likely that snakes are ‘forced’ out of habitats more rapidly by exotic shrubs than vines. Likewise, Japanese stiltgrass exhibits a similar pattern of invasion at Clifty, with average heights around 120cm in June, when males and females are most abundant in habitats that are highly prone to its invasion. Thus, exotic shrubs, Japanese stiltgrass, and, to some extent, oriental bittersweet appear to exert significant effects on males. Nongravid females appear to be influenced by each of these species/groups in a similar manner, but oriental bittersweet may play a more substantial role by eliminating the forest canopy gaps that nongravid females most often utilize. Oriental bittersweet has been positively associated with canopy gaps in other studies (McNab and Loftis, 2002), and my observations at Clifty suggest that oriental bittersweet is most abundant at the mid- to overstory canopy level within forest canopy gaps, effectively eliminating several gaps that were used by nongravid females over the course of the study. As previously discussed, oriental bittersweet may also be have a sizeable effect on gravid females given the low thermal quality of oriental bittersweet as well as its propensity to occur on glades and within forest gaps at Clifty.

Ailanthus altissima (referred to herein as ailanthus) is one exotic species for which effects were especially difficult to quantity, and I did not include it herein. However, there exist ongoing efforts at Clfity being carried out by the Division of Nature Preserves to control ailanthus. These efforts began in the early 1990’s (personal communications, Richard Davis and Jason Larson, Indiana Department of Natural Resources), and the primary areas where most efforts have focused, somewhat unsuccessfully so far, are each relic glades that are used extensively by gravid copperheads. Ailanthus is an aggressive invader of open canopy and disturbed sites (Knap and Canham, 2000), posing a significant threat to all of the habitats utilized by copperheads. From a purely observational perspective, ailanthus appears to have eliminated several sites that were previously used by gravid females during gestation. While it has eliminated several additional basking sites used by nongravid individuals, it appears to be one of the species of greatest impact for gravid copperheads and, for these reasons, it should not go unmentioned.

Potential Impacts on Hibernation

One characteristic that is shared by most exotic species at Clifty (and elsewhere) is an extended growing season compared to most native vegetation. Harrington and coworkers demonstrated an extended growing season by some exotic shrubs, including bush honeysuckle (*Lonicera* spp.), compared to their native counterparts (1989). At Clifty, species such as privet and both honeysuckles were recorded to begin leafing out during the first week of March (or earlier) and hold their foliage well after the last snake returned to its hibernaculum in November. Examining Figures 2.9 – 2.12 indicates that this may have some impact on thermal properties, evident from the rightward shift of curves. Most native vegetation would not have foliage during the transitional periods for copperheads in the spring and fall, when copperheads are typically utilizing exposed talus and outcrops on south to west facing slopes (Chapter One; Minton, 2001; Smith *et al.*, 2009). The presence of exotic plants, especially shrubs, introduces a novel thermal constraint that may not be easily reconciled by snakes as they no longer have access to ridge-top canopy gaps and are limited to being in close proximity to hibernacula, which are often also heavily invaded by exotic shrubs. This may impact emergence times in the spring as well as the ability to acclimate properly following spring emergence. Some preliminary observations of emergence by copperheads suggest that snakes utilizing hibernacula with denser shrub and vine cover tend to exhibit a delayed emergence and/or dispersal based on lower operative environmental temperatures at hibernacula during typical periods of emergence and dispersal (Figs. A.1 & A.2). Further research is warranted in this area.

Additional Factors Affecting Habitat Selection

Undoubtedly, exotic plants are not limited to impacting copperheads and other ectotherms based solely on thermoregulation. Some exotic species may even enhance habitats such as glades on rare occasions by serving as refuge sites for snakes. Exotic vegetation at low density and/or height seems to provide a filter layer from intense sun exposure just as native vegetation might (Diaz, 1994), potentially maintaining higher temperatures during night than nearby habitats lacking vegetation. The case of Japanese honeysuckle occurring in sparse patches at low densities and heights on glades is an example of this scenario. Johnson grass and crownvetch are each additional species that tend to grow in sparse patches and lower heights, respectively, in glade habitats. Each of these species were also higher in overall mean T_e than other exotic habitats. Despite this fact, the somewhat minimum impact that a few of these invaders have in some glade situations does not compensate for their overall effects in non-glade habitats nor for the potential for further invasion in glade habitats.

Mechanisms beyond thermoregulation may involve prey availability and/or foraging success apparent from a negative relationship between foraging success and invasion level. However, given that copperheads avoided invasive plants at multiple spatial scales, a negative correlation between foraging and density of exotic plants might be expected based simply on the amount of time copperheads spent in each habitat. A negative relationship between leaf litter depth and exotic vegetation density within the forest interior also suggested that at least some exotic plants may have an effect on rates of leaf litter decomposition. Given a positive relationship between increased leaf litter depth and copperhead occurrence as well as the potential importance that leaf litter serves as a concealment factor and as a suitable habitat for copperhead prey species (which include a substantial number of invertebrate species) (Fitch 1960; Minton 2001; Reinert 1984; Smith *et al.,* 2009), this effect may be a significant factor driving avoidance. Aston *et al*. (2005) demonstrated that accelerated decomposition rates occurred in woody exotic habitats, including those partially composed of bush honeysuckle, in comparison to native stands, providing some additional support for this possible effect.

Quantifying Thermal Quality

The conventional method of quantifying thermal quality using average deviations from the upper and lower bound of the preferred body temperature assumes that habitat with temperatures above the upper bounds are equivalent in terms of thermoregulatory constraints to those with temperatures falling below the lower bounds. Support for this assumption comes from the concept of time constraints, in which an ectotherm must invest time in seeking refuge from high temperatures and thus forgoing mating or foraging opportunities for example (Hertz *et al*., 1993; Blouin-Demers and Weatherhead, 2001). I was concerned primarily with T_e falling below the preferred body temperature range rather than exceeding it. Since copperheads are crepuscular during cooler periods and primarily nocturnal during summer, time constraints related to refuge use during daylight hours are probably of very low significance. A more critical dilemma for copperheads probably lies in an increasing need to bask when temperatures are too low and thus increased risk of exposure to predators. This may be especially true when contiguous areas are uniformly low in thermal quality and finding thermally advantageous microhabitats is not an option within many exotic macrohabitats. In such a scenario, traveling relatively long distances to more thermally suitable macrohabitats is the only alternative to remaining below the preferred body temperature range since the entire macrohabitat in question is considered low quality. Moreover, when operative temperatures within any habitat exceeded the upper bounds of the preferred body temperature range, refuge temperatures within the warmest habitat at the same time never exceeded the upper bound of T_{pref}, even on the hottest days of the year in 2010 and 2011 (Fig. 2.14 – 2.15). Therefore, selecting a habitat that exceeds the preferred body temperature range at the surface during some periods is probably superior in terms of energetics (and presumably fitness) to one that rarely provides operative temperatures that reach the lower bounds of the preferred body temperature range. Despite this contention, d_e provided results that were in overall agreement with other methods concerning the thermal quality of exotic plant habitats, which provides strong support for the impacts of exotic plants on thermoregulation since the extremely high operative temperatures in glade habitats, for example, did not deem glades lower in quality than any exotic habitats. Indeed, glade habitats were ranked at or near the top for gravid and nongravid individuals, respectively, when utilizing d_e as a measure of thermal quality.

Conclusions

Ultimately, multiple forms of exotic vegetation were negative predictors of copperhead habitat use at multiple spatial scales, suggesting that copperheads are heavily influenced by the presence of these invaders. I assumed that structurally similar species growing under similar habitat conditions would be equivalent in terms of thermoregulatory limitations and thus avoidance. This method did not permit an assessment of non-thermal effects and made avoidance of particular species by copperheads difficult to quantify at this point. General observations, however, suggest that the most prevalent species that were considered are avoided at some level, with the exception of Japanese honeysuckle, which exhibits widespread but extremely diffuse growth patterns at Clifty. Avoidance is broadly corroborated by multiple measures of thermal quality. The most biologically relevant measures (*i.e.*, proportion exceeding the lower bound of T_{pref} as well as d_e) place mixed exotic habitats as the lowest quality overall and exotic shrubs as the lowest quality as group, with six different species that each exert similar potential thermal constraints on copperheads (privet, autumn olive, bush honeysuckle, jetbead, wineberry, and Armenian blackberry). Only one exotic vine and one exotic herbaceous exhibited comparable levels of low thermal quality, which include oriental bittersweet and Japanese stiltgrass (Fig. 2.10, 2.11, 2.13). That each of the aforementioned species/groups are the most prevalent exotic vegetation types exhibiting dense growth patterns at Clifty suggests that any species exhibiting dense growth patterns is probably of low thermal quality in comparison to their native counterparts, as might be expected. Thus species such as Johnson grass and Japanese honeysuckle that did not occur in large, dense monocultures at Clifty surely have the potential to reduce thermal quality in any site where they do exhibit such patterns. However, species such as crownvetch, at least at Clifty, probably occur at stem densities and heights that allow sufficient sunlight to warm temperatures nearer the ground given that measured sites were comprised of dense monocultures in each case.

Admittedly, the thermal quality of many habitats was probably highly dependent on the greater landscape in which they occurred. I attempted to match each biophysical model set in the field by terrain features and exposure, but taking into account all landscape features affecting thermal regimes is a daunting task that I did not attempt to achieve. Models placed in closed-canopy forest sites were intentionally biased in targeting habitats with 100% overstory and midstory canopy closure (which includes the majority of what is left of natural forest communities at Clifty). The fact that most exotic monocultures were lower in thermal quality than closed-canopy forest while occurring in open-canopy habitats (glades, old fields, and forest gaps) provides strong support for significant exotic plant influences on thermal regimes and the thermoregulatory opportunities available to copperheads. Each of the species investigated herein are also known to occur at high densities in more forested settings at Clifty and elsewhere, and copperheads are known to prefer forested landscapes across their range, sometimes selecting forest exclusively (Chapter One). However, copperheads at Clifty show little preference for most forest habitats. Operative environmental temperatures in exotic plant monocultures in these more forested habitats are certainly much lower than monocultures occurring in more open habitats. Considering this, it is likely that exotic plants have caused an overall reduction in thermally preferable/suitable habitat that is more extensive than currently known. Unfortunately, it is now difficult to quantify these effects without knowing the thermal regimes in forested habitats before exotic plant invasions occurred. In either case, even species that were not considered thermally unsuitable for copperheads may have significant negative effects when they occur in forests.

One potential argument against the negative impacts of exotic plants on thermoregulation may involve projected climate warming patterns, where an increase in ambient temperature may increase operative environmental temperatures in some habitats to a suitable range. Over the next 50 years, ambient temperatures are projected to increase 2-4 °C across the eastern United States (Solomon *et al.,* 2007). Those species currently considered low in thermal quality will remain low in thermal quality when incorporating into T_e models a 3 °C increase in ambient temperature (Fig. A.3). Moreover, many exotic plants are expected to undergo range expansions owing to climate change (*e.g.*, Dukes and Mooney, 1999; Walther *et al*., 2002; Hellmann *et al*., 2008). This also suggests that copperhead populations currently occurring in warmer regions are likely facing similar thermal constraints due to exotic plant invasions, and those populations occurring in areas lacking most exotic species will likely be impacted under future climate change conditions.

In general, most exotic species discussed herein should have the greatest impact on gravid individuals when considering that gravid snakes are often very precise thermoregulators with higher preferred body temperatures than nongravid individuals. Gestation temperature is believed to affect the development of embryos (Tu and Hutchison, 1994; Gregory *et al*., 2006). Like many other ectotherms, gravid copperheads also have higher preferred body temperatures than do nongravid females or males, and the operative temperatures within most exotic vegetation habitats impose the greatest potential thermal constraints on these individuals (Table 2.6 & 2.7). This is true in terms of both d_e and daily temperatures reaching the lower bounds of T_{pref}. Moreover, any thermal constraints imposed by exotics plants on any sex/reproductive group affects physiological performance and thus, even if only short-term, the fitness of an individual. Therefore, this study provides strong support for the preliminary assessment that recent copperhead declines are associated with the introduction and proliferation of exotic plants.

Table 2.1.

Occurrence rates for exotic plant species within one-meter random plots at the landscape level and mean (± SE) occurrence rate in one-meter random plots within the activity range for males, nongravid females, and gravid females at Clifty Falls State Park. Grey highlighting indicates a higher occurrence rate within the activity range of copperheads than at the broader landscape level.

Common Name	Scientific Name	Landscape	Activity Range		
			Male	Female	Gravid
Garlic mustard	*Allaria petiolata* (Bieb.) Cavara & Grande	0.520	0.322 (0.021)	0.458 (0.028)	0.323 (0.029)
Oriental bittersweet	*Celastrus orbiculatus* Thunb.	0.366	0.310 (0.021	0.420 (0.028)	0.358 (0.030)
Jpn. honeysuckle	*Lonicera japonica* Thunb.	0.361	0.485 (0.023)	0.603 (0.028)	0.615 (0.030)
Privet(s)	*Ligustrum* spp	0.351	0.371 (0.022)	0.438 (0.028)	0.420 (0.031)
Multiflora rose	*Rosa multiflora* Thunb.	0.146	0.108 (0.014)	0.099 (0.017)	0.035 (0.011)
Star-of-Bethlehem	*Ornithogalum umbellatum* Linneaus	0.108	0.020 (0.006)	0.032 (0.010)	0.023 (0.009)
Jpn. stiltgrass	*Microstegium vimineum* (Trin.) Camus	0.092	0.075 (0.012)	0.067 (0.014)	0.047 (0.013)
Autumn olive	*Eleaganus umellata* Thunb.	0.080	0.092 (0.013)	0.054 (0.013)	0.023 (0.009)
B. honeysuckle(s)	*L. maackii* (Rupr.) Herder; *L.* x *bella* Zabel	0.071	0.075 (0.012)	0.080 (0.015)	0.097 (0.018)
Tree of heaven	*Ailanthus altissima* (P. Mill.) Swingle	0.065	0.073 (0.012)	0.090 (0.016)	0.078 (0.017)
Arm. blackberry	*Rubus armeniacus* Focke	0.032	0.041 (0.009)	0.013 (0.006)	<0.001
Wine raspberry	*R. phoenicolasius* Maxim	0.022	0.024 (0.007)	0.010 (0.006)	0.016 (0.008)
Ground ivy	*Glechoma hederacae* Linnaeus	0.019	0.018 (0.006)	0.010 (0.006)	< 0.001
Jetbead	*Rhodotypos scandens* (Thunb.) Makino	0.017	0.024 (0.007)	0.032 (0.010)	0.008 (0.005)
Johnson grass	*Sorghum halepense* Pers.	0.017	0.061 (0.011)	0.026 (0.009)	0.016 (0.008)
Wing. burning bush	*Euonymus alatus* (Thunb.) Siebold	0.015	0.002 (0.002)	0.010 (0.006)	0.004 (0.004)
Periwinkle	*Vinca minor* Linnaeus	0.011	0.006 (0.004)	0.035 (0.010)	0.008 (0.005)
Crownvetch	*Coronilla varia* Linnaeus	0.004	0.024 (0.007)	<0.001	0.008 (0.005)
Mahaleb cherry	*Prunus mahaleb* Linnaeus	0.004	< 0.001	0.003 (0.003)	0.047 (0.013)
Canada thistle	*Cirsium arvense* (L) Scop.	0.004	0.002 (0.002)	< 0.001	0.004 (0.004)
Winter creeper	*E. fortunei* (Turcz.) Hand. –Mazz.	0.004	0.002 (0.002)	0.010 (0.006)	0.004 (0.004)
Com. mullein	*Verbascum Thapsus* Linneaus	0.002	0.002 (0.002)	< 0.001	< 0.001
English ivy	*Hedera helix* Linneaus	0.002	< 0.001	0.003 (0.003)	0.004(0.004)
Moneywort	*Lysimachia nummularia* Linneaus	0.002	0.004 (0.002)	< 0.001	< 0.001
Silk tree	*Albizia julibrissin* Durazz.	< 0.000	0.002 (0.002)	0.003 (0.003)	< 0.001
Com. teasel	*Dipsacus sylvestris* Huds.	< 0.000	0.002 (0.002)	< 0.001	< 0.001
Norway maple	*Acer platanoides* Linnaeus	< 0.000	< 0.001	< 0.001	< 0.001
Princess tree	*Paulownia tomentosa* (Thunb.) Sieg. & Zucc.	< 0.000	0.010 (0.005)	0.003 (0.003)	0.020 (0.009)
White mulberry	*Morus alba* Linneaus	< 0.000	< 0.001	< 0.001	< 0.001
Jpn. barberry	*Berberis thunbergii* D.C.	< 0.000	< 0.001	< 0.001	< 0.001

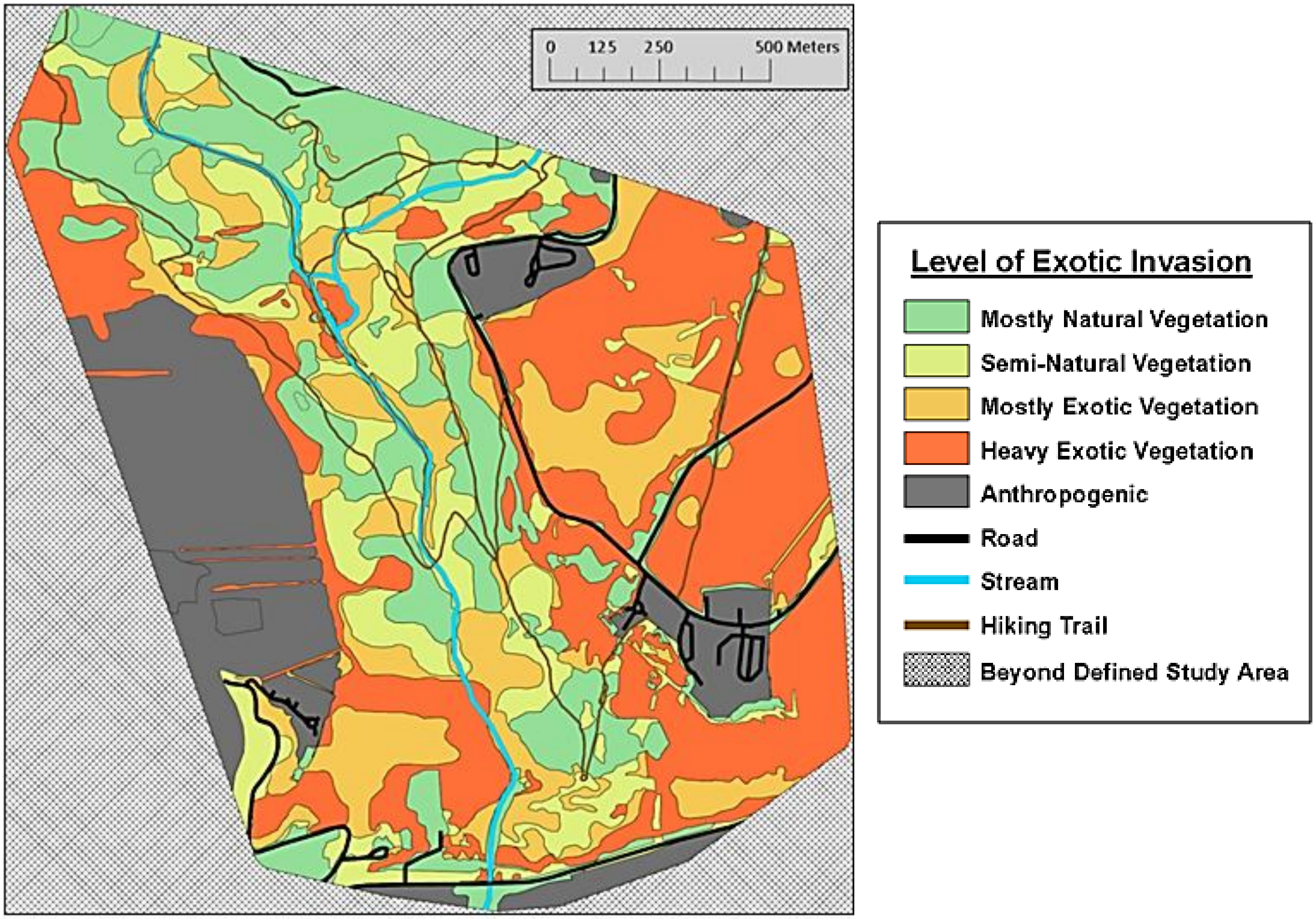

Figure 2.1. The level of exotic vegetation invasion at Clifty Falls State Park during the 2011 field season. Exotic plants and native habitats were mapped in the field during the 2009, 2010, and 2011 field seasons using global positioning systems and hand-drawn maps.

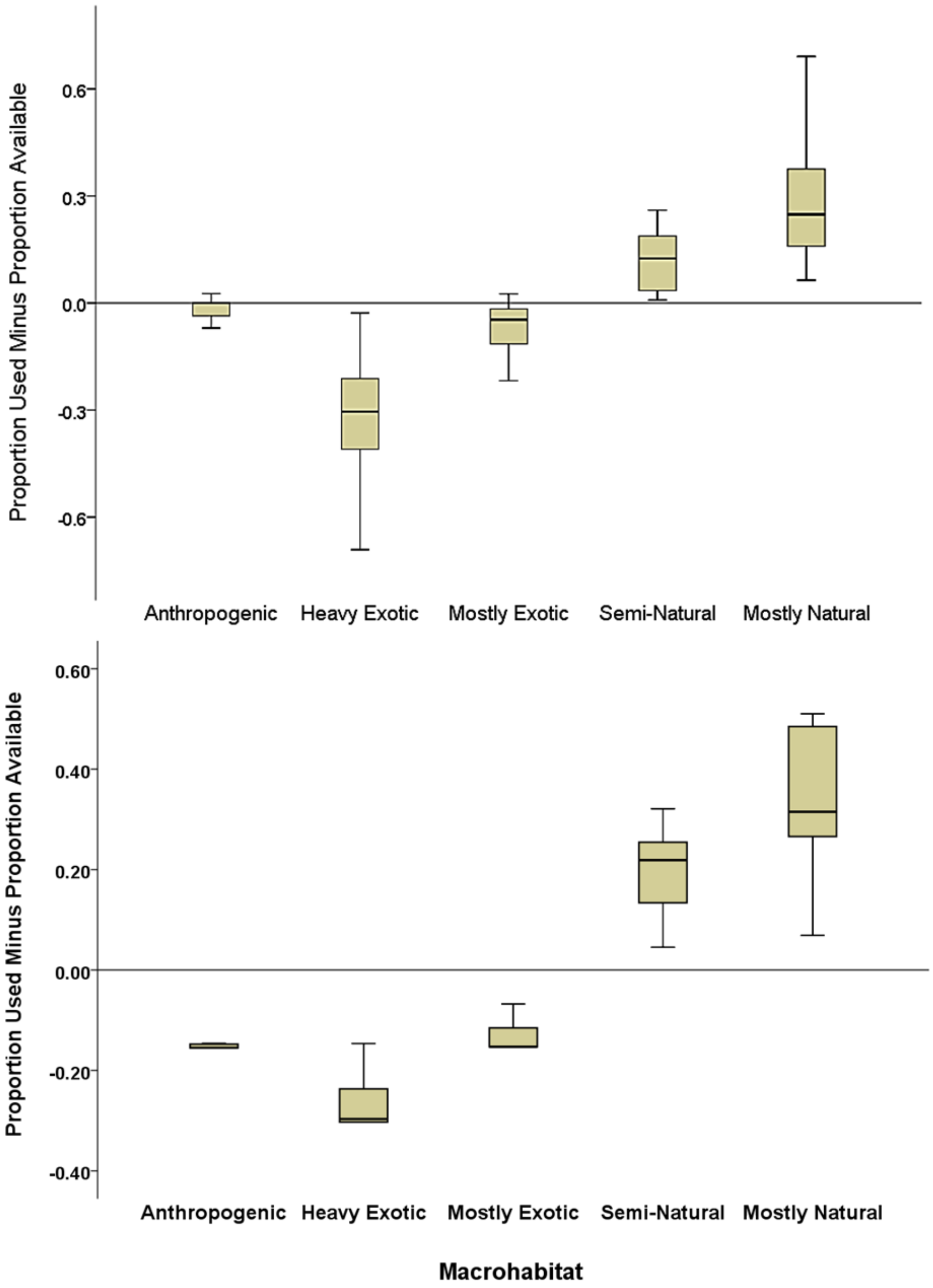

Figure 2.2. Boxplots of differential use and availability of different levels of exotic invasion and anthropogenic habitat at the activity range (top) and landscape level (bottom) for Northern Copperheads at Clifty Falls State Park. Values above zero indicate preference, whereas values below zero indicate avoidance. Error bars represent 95% confidence intervals about the mean.

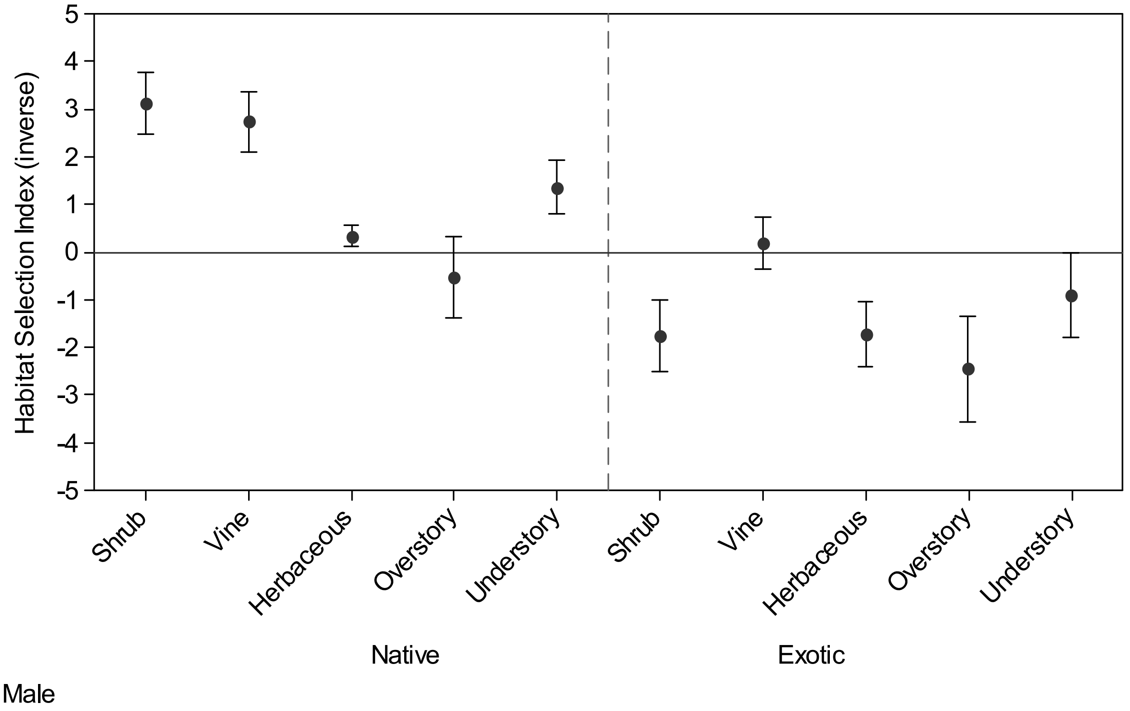

Figure 2.3. Index of habitat selection for distance to nearest vegetation (intermediate scale selection) for male Northern Copperheads at Clifty Falls State Park. Points represent the inverse of the mean difference between each snake location and random point pair for distance to nearest vegetation type. Values above zero indicate positive selection whereas values below zero indicate negative selection. Error bars represent two standard errors above and below the mean.

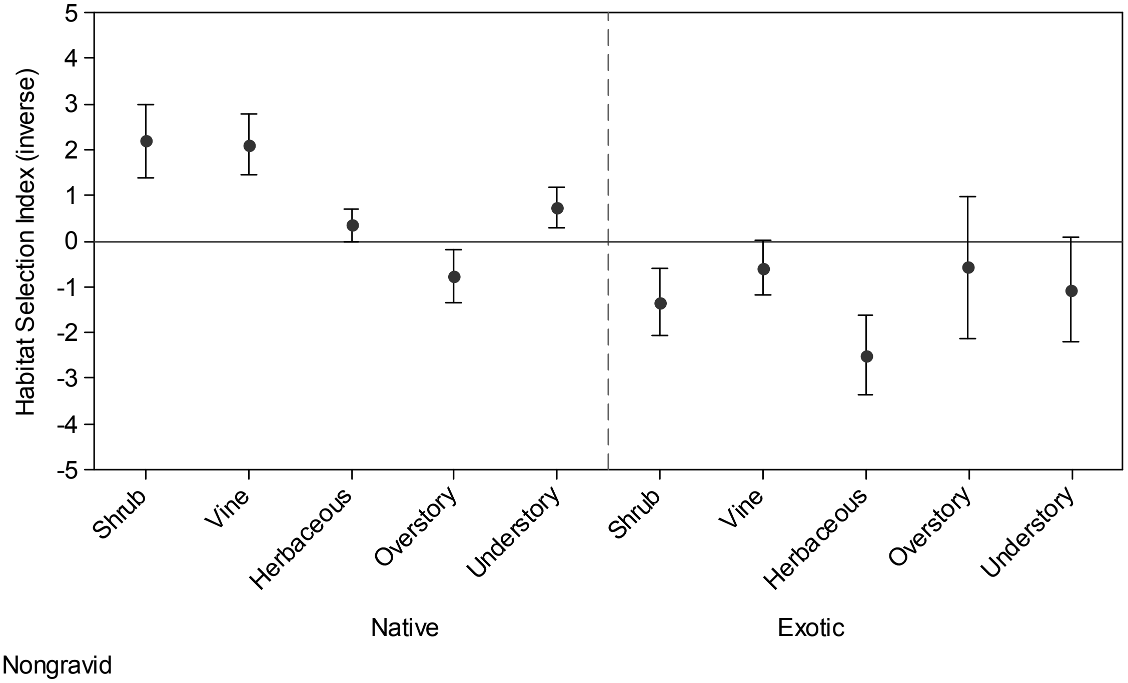

Figure 2.4. Index of habitat selection for distance to nearest vegetation (intermediate scale selection) for nongravid female Northern Copperheads at Clifty Falls State Park. Points represent the inverse of the mean difference between each snake location and random point pair for distance to nearest vegetation type. Values above zero indicate positive selection whereas values below zero indicate negative selection. Error bars represent two standard errors above and below the mean.

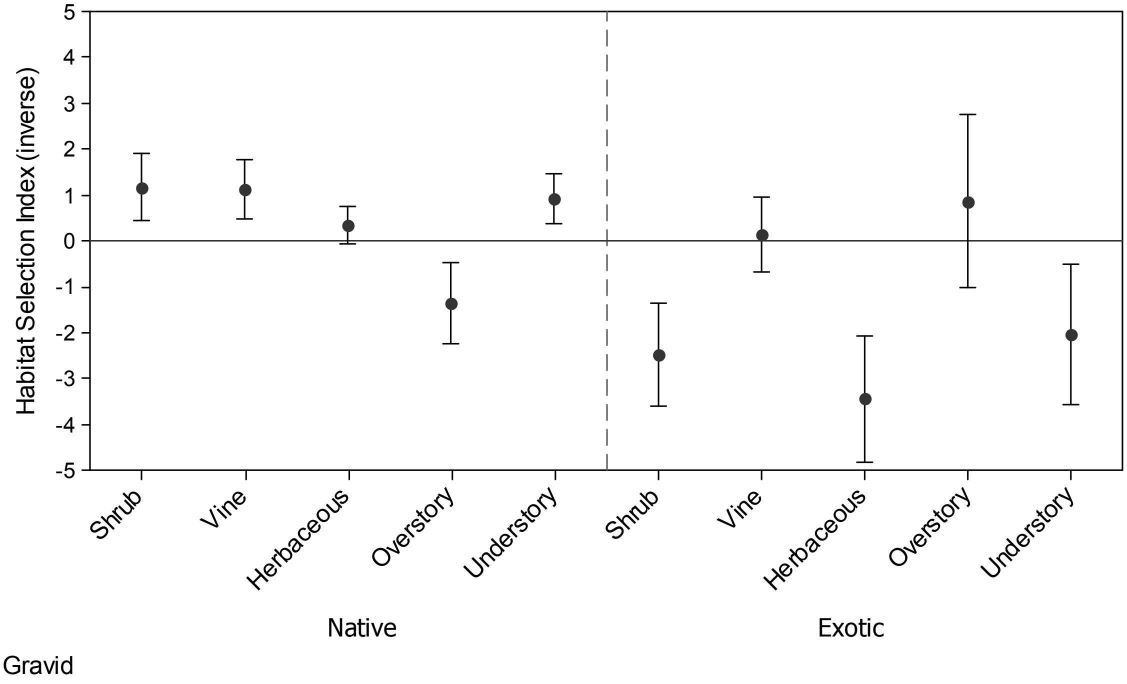

Figure 2.5. Index of habitat selection for distance to nearest vegetation (intermediate scale selection) for gravid female Northern Copperheads at Clifty Falls State Park. Points represent the inverse of the mean difference between each snake location and random point pair for distance to nearest vegetation type. Values above zero indicate positive selection whereas values below zero indicate negative selection. Error bars represent two standard errors above and below the mean.

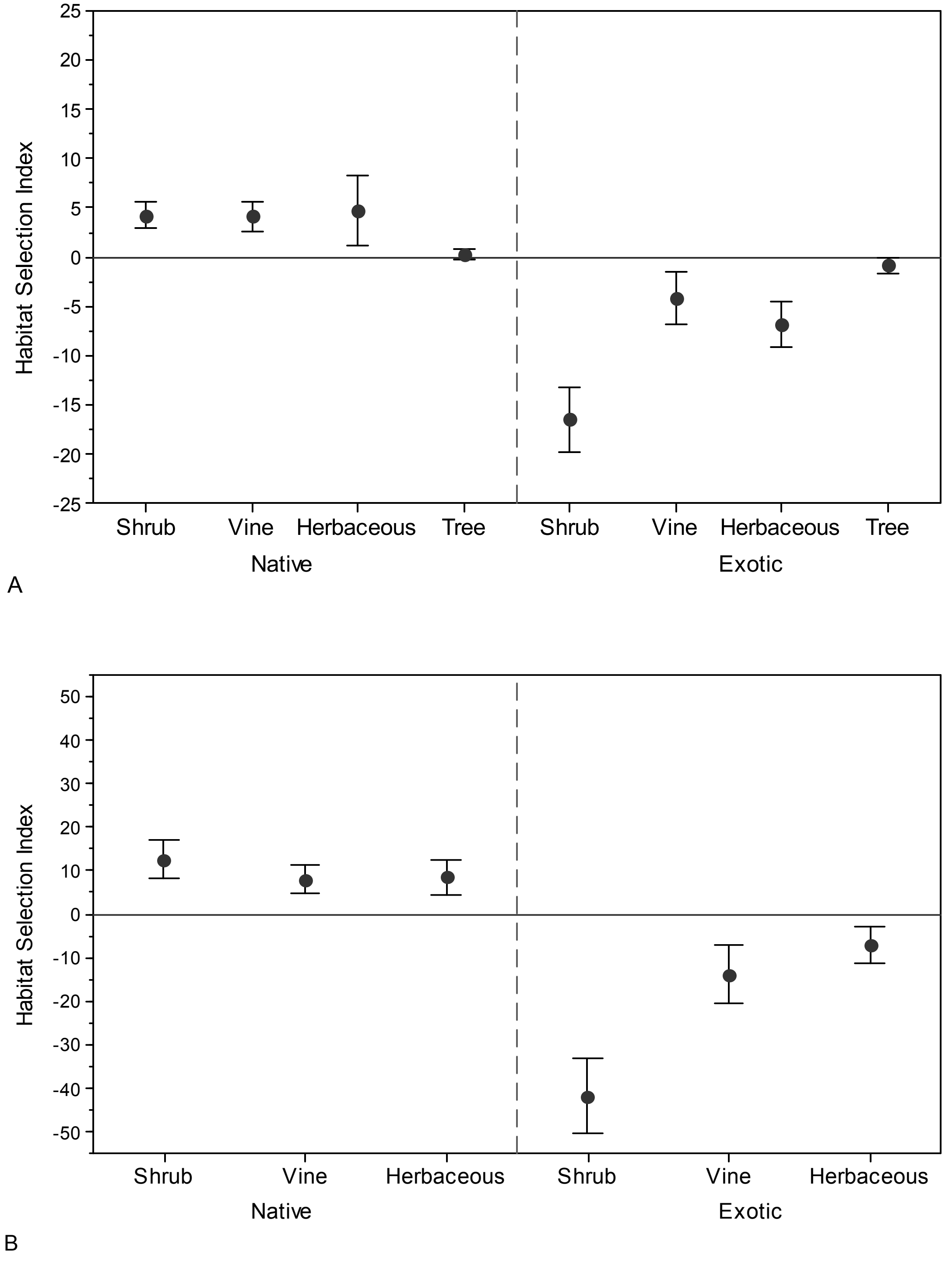

Figure 2.6. Index of habitat selection for density (A) and height (B) (fine-grained selection) for male Northern Copperheads at Clifty Falls State Park. Points represent the mean difference (± 2 SE) between each snake location and random point pair.

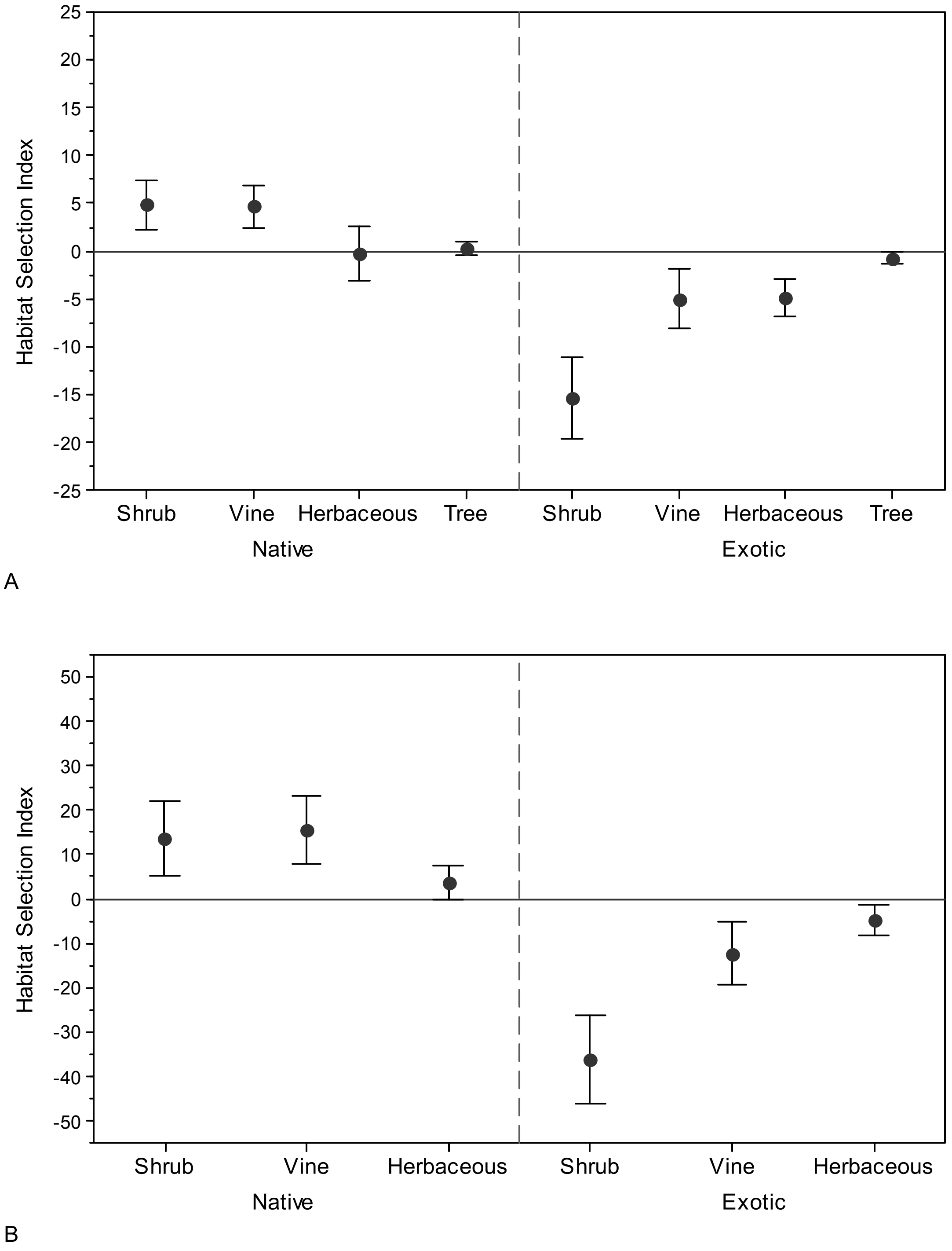

Figure 2.7. Index of habitat selection for density (A) and height (B) (fine-grained selection) for nongravid female Northern Copperheads at Clifty Falls State Park. Points represent the mean difference (± 2 SE) between each snake location and random point pair.

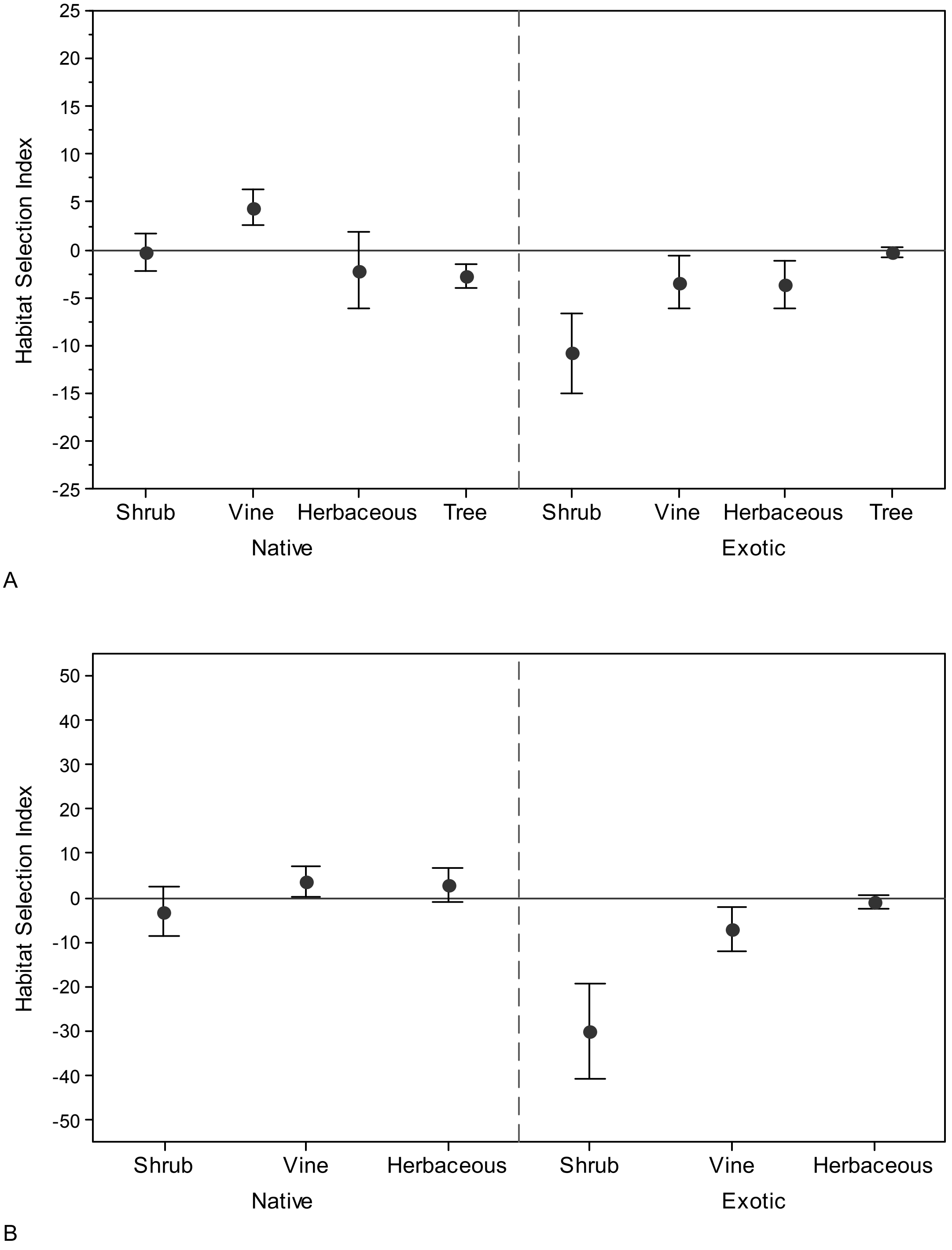

Figure 2.8. Index of habitat selection for density (A) and height (B) (fine-grained selection) for gravid female Northern Copperheads at Clifty Falls State Park. Points represent the mean difference (± 2 SE) between each snake location and random point pair.

Table 2.2. Intermediate-scale habitat selection models for gravid female, nongravid female, and male Northern Copperheads at Clifty Falls State Park supported by AIC_c. Values are included for AIC_c, ΔAIC_c, McFadden's ρ^2, and overall model significance based on likelihood ratio tests.

Model	AIC_c	ΔAIC_c	ρ^2	*P*
Gravid Female				
can + *gap* + *nat.shrub* + *nat.under* + *ex.shrub* + *ex.herb*	75.045	-	.689	< .001
Nongravid Female				
can + *gap* + *nat.shrub* + *nat.vine* + *ex.shrub* + *ex.herb* + *ex.over.dbh*	183.092	-	.457	< .001
can + *gap* + *nat.shrub* + *nat.vine* + *ex.shrub* + *ex.herb*	183.483	0.391	.449	< .001
can + *gap* + *nat.shrub* + *nat.vine* + *ex.shrub* + *ex.herb* + *nat.under*	184.673	1.581	.452	< .001
can + *gap* + *nat.shrub* + *nat.vine* + *ex.shrub* + *ex.herb* + *nat.under* + *ex.over.dbh*	184.529	1.437	.460	< .001
Male				
can + *gap* + *nat.shrub* + *nat.vine* + *ex.shrub* + *ex.herb* + *ex.over*	298.417	-	.434	< .001
can + *gap* + *nat.shrub* + *nat.vine* + *nat.herb* + *ex.shrub* + *ex.herb* + *ex.over*	300.157	1.740	.435	< .001

Table 2.3. Fined-grained microhabitat selection models for male, nongravid female, and gravid female Northern Copperheads at Clifty Falls State Park supported by AIC_c. Values are included for AIC, ΔAIC (relative to minimum), and McFadden's ρ^2.

Model	AIC_c	ΔAIC_c	ρ^2
Gravid Female			
nat.tree + *nat.vine.ht* + *ex.herb* + *ex.shrub.ht* + *ex.vine.ht*	122.868	-	.456
nat.tree + *nat.vine* + *ex.herb* + *ex.shrub.ht* + *ex.vine.ht*	123.950	1.082	.450
Nongravid Female			
nat.shrub + *nat.vine* + *ex.herb* + *ex.shrub.ht* + *ex.vine.ht* + *ex.herb.ht*	206.908	-	.387
nat.shrub + *nat.vine* + *ex.herb* + *ex.shrub.ht* + *ex.vine.ht*	208.304	1.396	.376
Male			
nat.shrub + *nat.vine* + *nat.vine.ht* + *nat.herb.ht* + *ex.herb* + *ex.shrub.ht*	300.024	-	.412
nat.shrub + *nat.vine* + *nat.shrub.ht* + *nat.vine.ht* + *nat.herb.ht* + *ex.herb* + *ex.shrub.ht*	300.079	.055	.416
nat.shrub + *nat.vine* + *nat.shrub.ht* + *nat.vine.ht* + *nat.herb.ht* + *ex.herb* + *ex.shrub.ht* + *ex.vine.ht*	301.750	1.726	.418

Table 2.4. Final paired logistic regression models for intermediate-scale habitat selection by gravid female, nongravid female, and male Northern Copperheads supported by AIC_c and parameter significance.

Variable	Coefficient	SE	Odds Ratio (95% CI)	Unit Increase (odds ratio)
Gravid Females				
canopy	-.059	.019	.942 (.908,.977)	1%
gap	2.823	.971	16.825 (2.507, 112.903)	(≥ 30% gap)
nat.shrub	-.276	.123	.759 (.596, .966)	1m
nat.under	-.943	.249	.389 (.239, .635)	1m
ex.shrub	.358	.099	1.430 (1.177, 1.736)	1m
ex.herb	.100	.050	1.105 (1.002, 1.219)	1m
Nongravid Females				
canopy	-.023	.008	.978 (.962, .993)	1%
gap	1.072	.385	2.921 (1.373, 6.212)	(≥ 30% gap)
nat.shrub	-.155	.055	.856 (.768, .955)	1m
nat.vine	-.390	.087	.677 (.569, .801)	1m
ex.shrub	.141	.058	1.152 (1.028, 1.290)	1m
ex.herb	.118	.038	1.122 (1.044, 1.212)	1m
ex.over.dbh	-.065	.043	.937 (.861, 1.020)	1cm
Males				
canopy	-.018	.006	.982 (.971, .993)	1%
gap	1.066	.313	2.905 (1.573, 5.364)	(≥ 30% gap)
nat.shrub	-.258	.047	.772 (.704, .848)	1m
nat.vine	-.146	.040	.864 (.799, .934)	1m
ex.shrub	.100	.028	1.105 (1.045, 1.168)	1m
ex.herb	.064	.025	1.066 (1.015, 1.121)	1m
ex.over	.032	.016	1.033 (1.001, 1.066)	1m

Table 2.5. Final paired logistic regression models for fine-grained microhabitat selection by gravid female, nongravid female, and male Northern Copperheads supported by AIC_c and parameter significance. Negative coefficients indicate negative selection, whereas positive coefficients indicate positive selection.

Variable	Coefficient	SE	Odds Ratio (95% CI)	Unit Increase (odds ratio)
Gravid Females				
nat.tree	-.308	.094	.735 (.611,.883)	1%
nat.vine.ht	.063	.017	1.065 (1.031, 1.101)	1cm
ex.herb	-.146	.059	.864 (.771, .971)	1%
ex.shrub.ht	-.053	.014	.948 (.923, .974)	1cm
ex.vine.ht	-.034	.014	.967 (.941, .994)	1cm
Nongravid Females				
nat.vine	.037	.018	1.037 (1.001, 1.075)	1%
nat.shrub.ht	.006	.003	1.006 (1.000, 1.013)	1cm
ex.herb	-.175	.043	.839 (.772, .912)	1%
ex.shrub.ht	-.013	.004	.988 (.981, .994)	1cm
ex.vine.ht	-.018	.008	.982 (.967, .997)	1cm
Males				
nat.shrub	.093	.026	1.097 (1.043, 1.155)	1%
nat.vine	.070	.032	1.072 (1.006, 1.1.143)	1%
nat.vine.ht	.020	.009	1.021 (1.002, 1.039)	1cm
nat.herb.ht	.019	.005	1.019 (1.009, 1.029)	1cm
ex.herb	-.030	.011	.971 (.951, .992)	1%
ex.shrub.ht	-.023	.004	.977 (.969, .986)	1cm

Table 2.6. Mean (± SE) body temperature and 75% and 25% quartiles of body temperatures selected by male, nongravid female, and gravid female Northern Copperheads in a laboratory thermal gradient.

Group	*n*	Mean T_b	25% Quartile	75% Quartile
Male	5	25.7 (± 0.5)	25.0 (± 0.6)	26.3 (± 0.6)
Nongravid Female	5	26.5 (± 0.2)	25.3 (± 0.5)	27.4 (± 0.3)
Gravid Female	5	27.6 (± 0.2)	26.9 (± 0.3)	28.5 (± 0.3)
Combined	15	27.6 (± 0.3)	25.7 (± 0.3)	27.4 (± 0.3)

Table 2.7. Mean (± SE), minimum, and maximum d_e during the activity season for male, nongravid female, and gravid female Northern Copperheads.

Group	Mean d_e	Minimum	Maximum
Male	8.15 (± 0.15)	6.99	8.75
Nongravid Female	8.38 (± 0.16)	7.11	9.02
Gravid Female	9.85 (± 0.18)	8.40	10.58

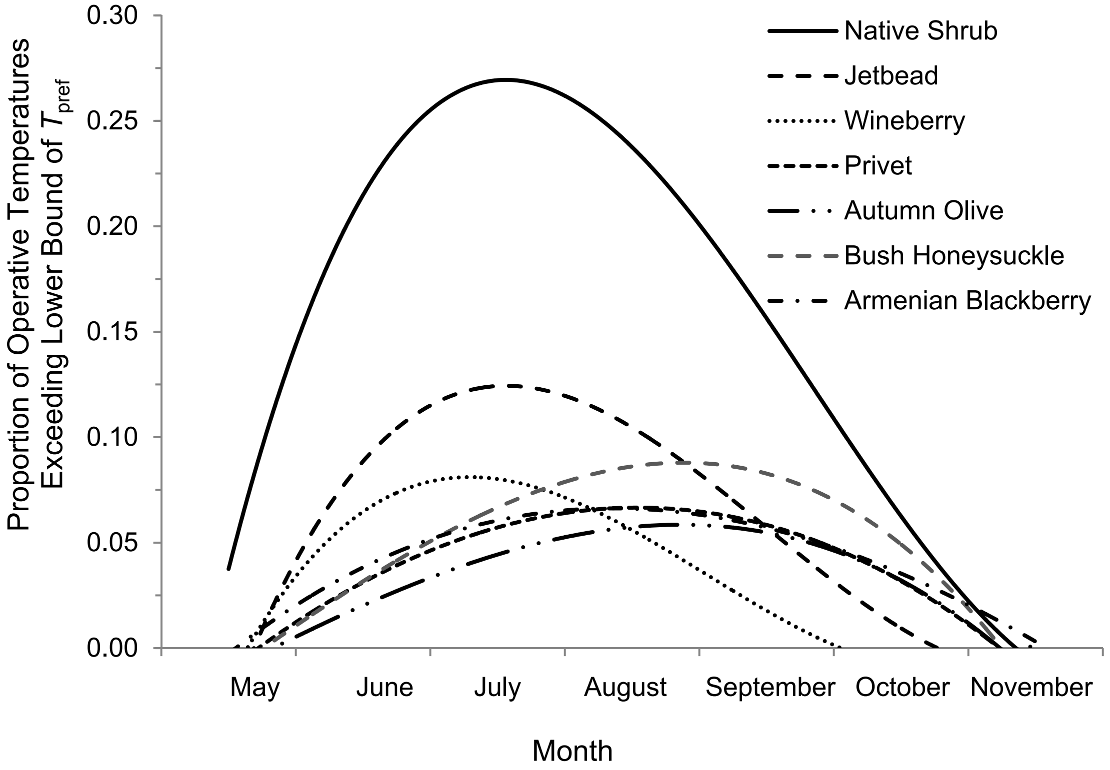

Figure 2.9. Third order polynomials fit to proportion of T_e exceeding the lower bounds of T_{pref} for native and exotic shrub habitats. Pairwise comparisons did not reveal any significant difference between any two exotic shrub species. Native shrub-dominated habitats were significantly higher in thermal quality than any exotic shrub-dominated habitat (Jetbead: $P < 0.0001$; Wineberry: $P < 0.0001$; Privet: $P < 0.001$; Autumn Olive: $P < 0.0001$; Bush Honeysuckle: $P = 0.002$; Armenian Blackberry: $P = 0.01$, Wilcoxon signed-rank tests corrected for multiplicity).

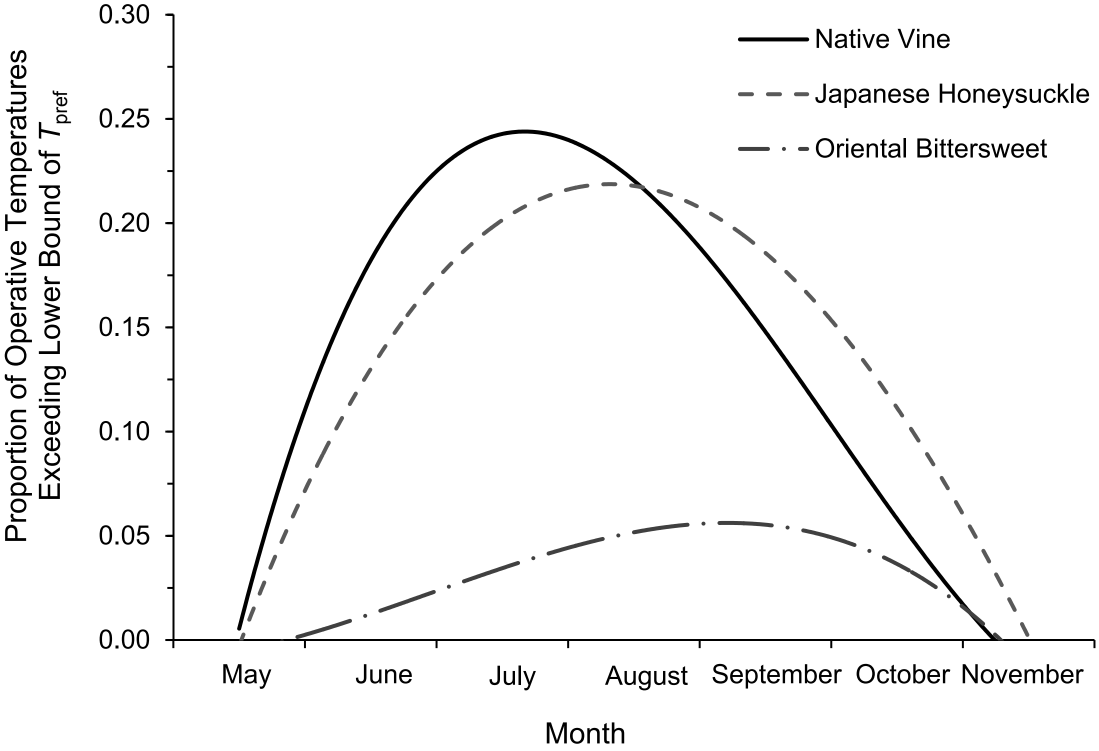

Figure 2.10. Third order polynomials fit to proportion of T_e exceeding the lower bounds of T_{pref} for native and exotic vine habitats. Native vine-dominated habitats were significantly higher in thermal quality than Oriental Bittersweet-dominated habitats (P = 0.003, Wilcoxon signed-rank test) but did not differ significantly from Japanese Honeysuckle-dominated habitats.

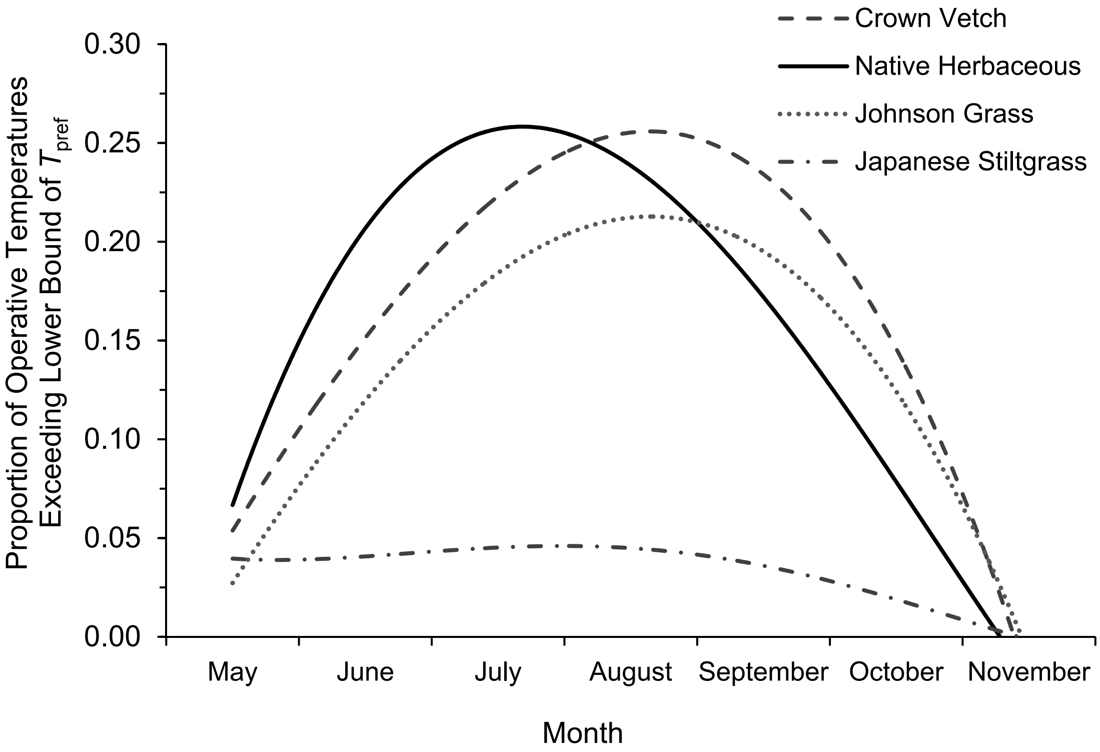

Figure 2.11. Third order polynomials fit to proportion of T_e exceeding the lower bounds of T_{pref} for native and exotic herbaceous habitats. Native herbaceous-dominated habitats were significantly higher in thermal quality than Japanese Stiltgrass-dominated habitats ($P = 0.024$, Wilcoxon signed-rank test) but did not differ significantly from Crownvetch or Johnson grass-dominated habitats.

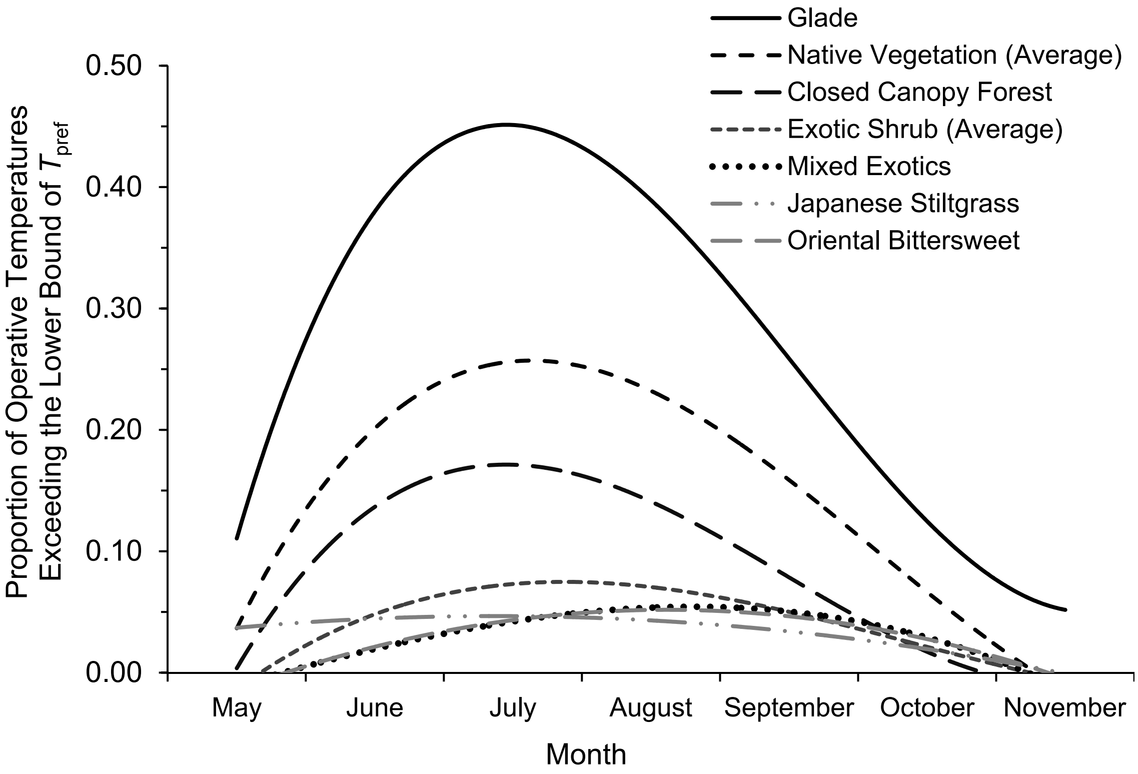

Figure 2.12. Third order polynomials fit to proportion of T_e exceeding the lower bounds of T_{pref} for native and exotic habitats. Glade habitats were significantly higher in thermal quality than any native vegetation habitat ($P < 0.001$, Wilcoxon signed-rank test). Mixed exotics, privet, autumn olive, wineberry, Armenian blackberry, jetbead, Japanese stiltgrass, and oriental bittersweet were each lower in thermal quality than closed-canopy forest, which was avoided by Northern Copperheads at Clifty Falls State Park.

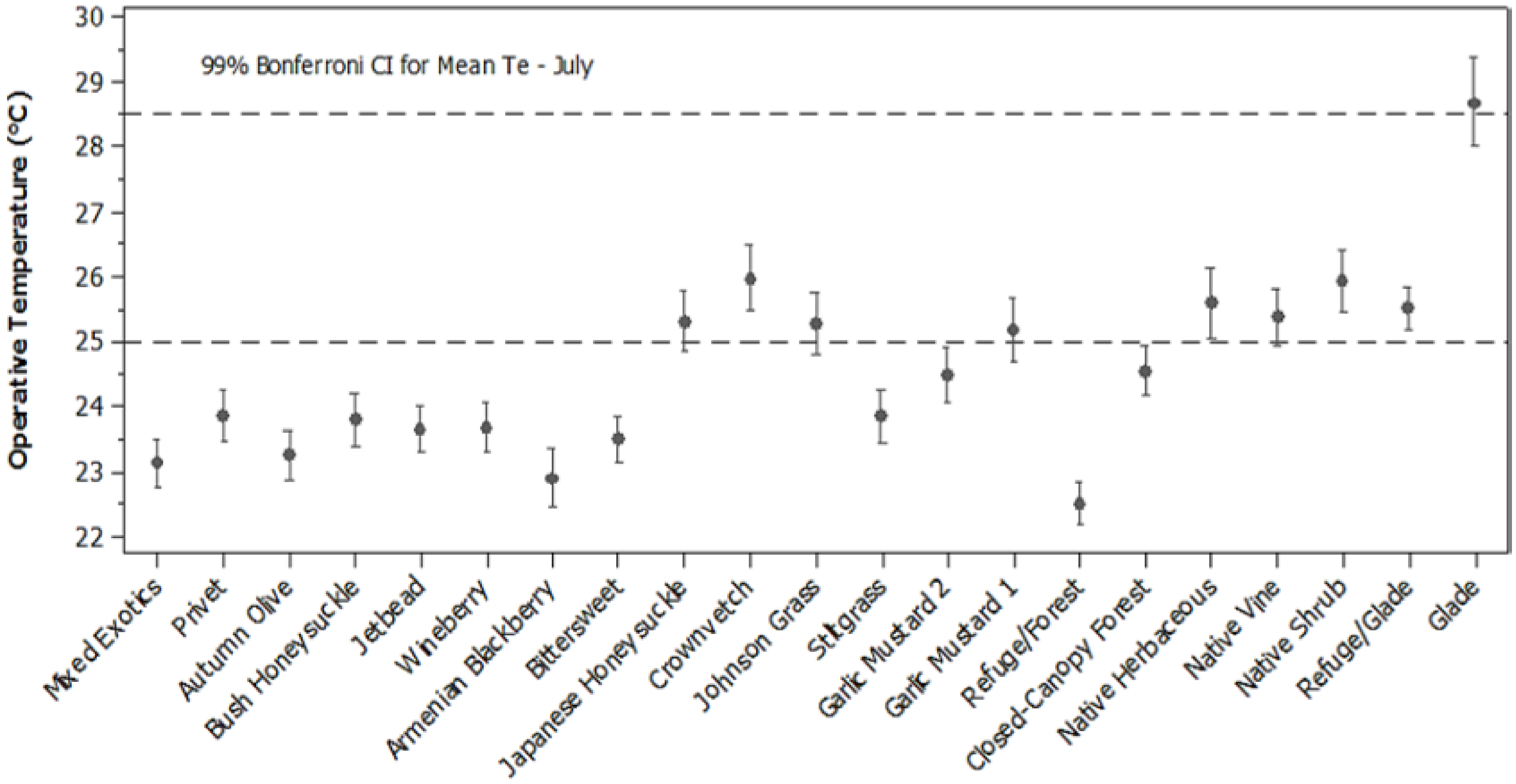

Figure 2.13. Mean proportion of operative environmental temperatures (T_e) exceeding the lower bounds of T_{pref} in habitats available to Northern Copperheads at Clifty Falls State Park during the warmest month (August) in 2010. Dotted lines represent the upper and lower extremes of the preferred body temperature range of Northern Copperheads. Error bars represent 99% confidence intervals with Bonferroni corrections applied.

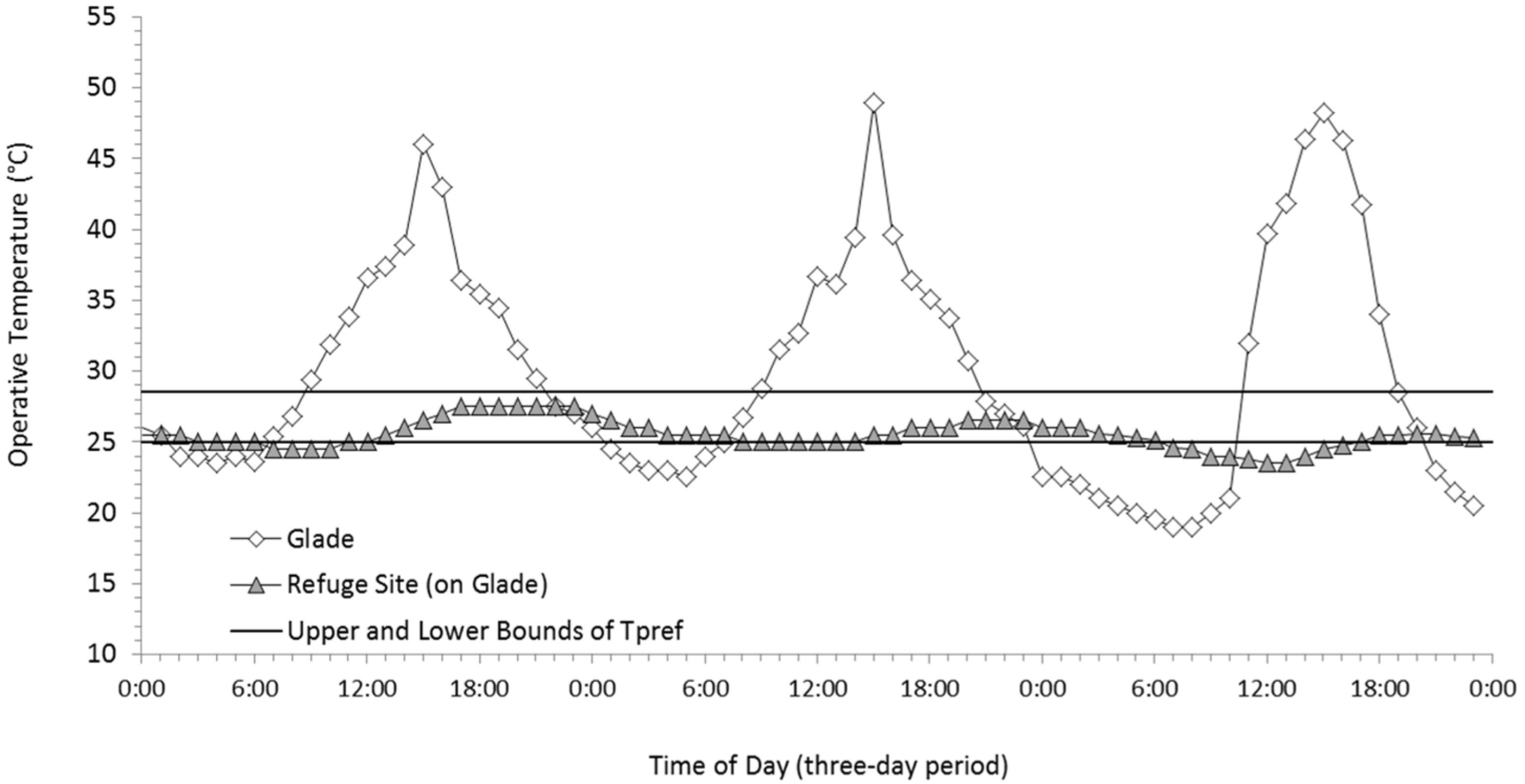

Figure 2.14. Operative environmental temperatures in glade habitats on bare ground (open triangle) and in refuge sites (solid triangles) during the warmest three days of the year in 2011 (June 3 – 5). Horizontal lines represent the maximum range of body temperatures preferred by Northern Copperheads.

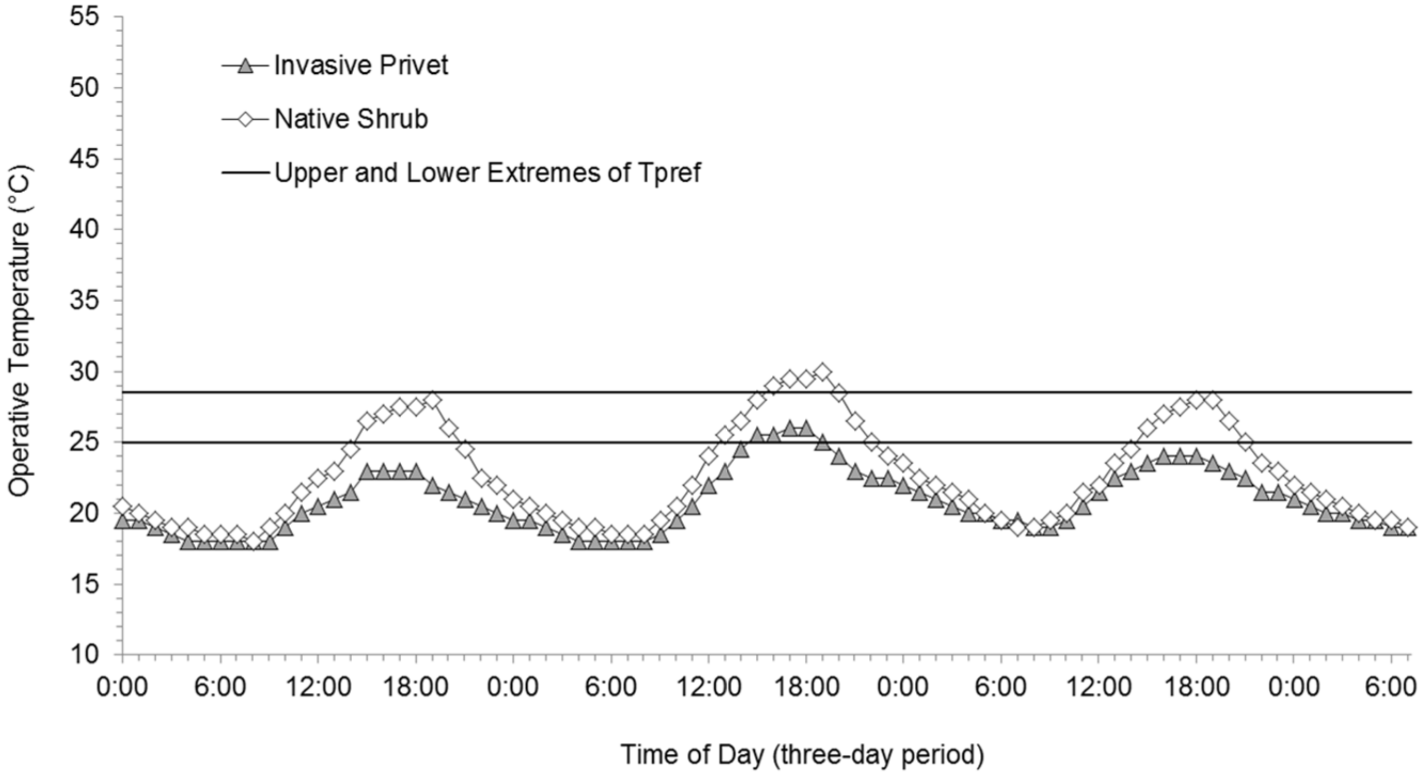

Figure 2.15. Operative environmental temperatures in native shrub (open triangle) and invasive privet (solid triangles) dominant habitats during the warmest three days of the year in 2011 (June 3 – 5). Horizontal lines represent the maximum range of body temperatures preferred by Northern Copperheads.

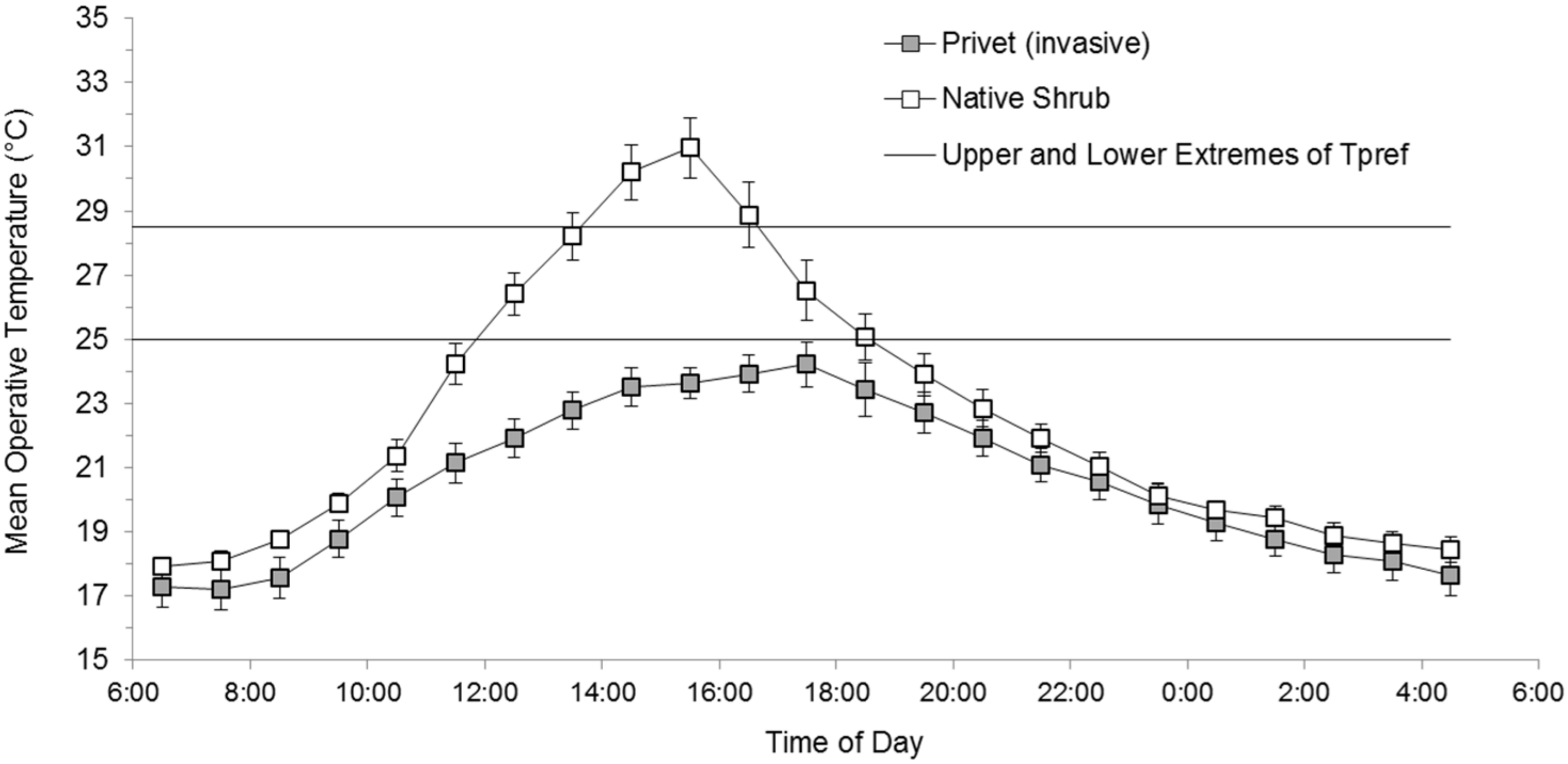

Figure 2.16. Mean daily temperatures experienced by a copperhead (operative environmental temperature) if it selected native shrub (open squares) or comparable privet-dominated (gray squares) habitats during the month of June.

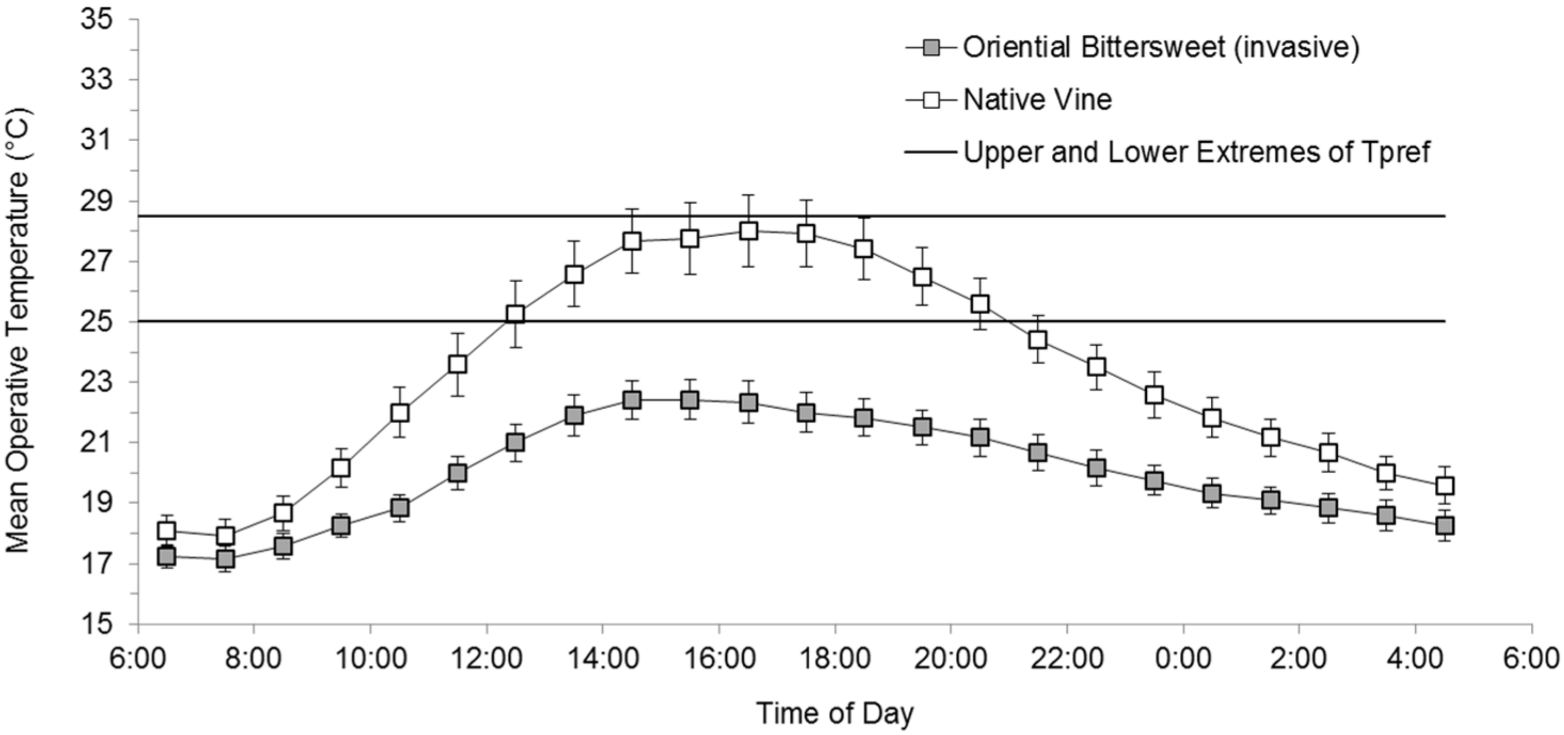

Figure 2.17. Mean daily temperatures experienced by a copperhead (operative environmental temperature) if it selected native vine (open squares) or comparable bittersweet-dominated (gray squares) habitats during the month of June.

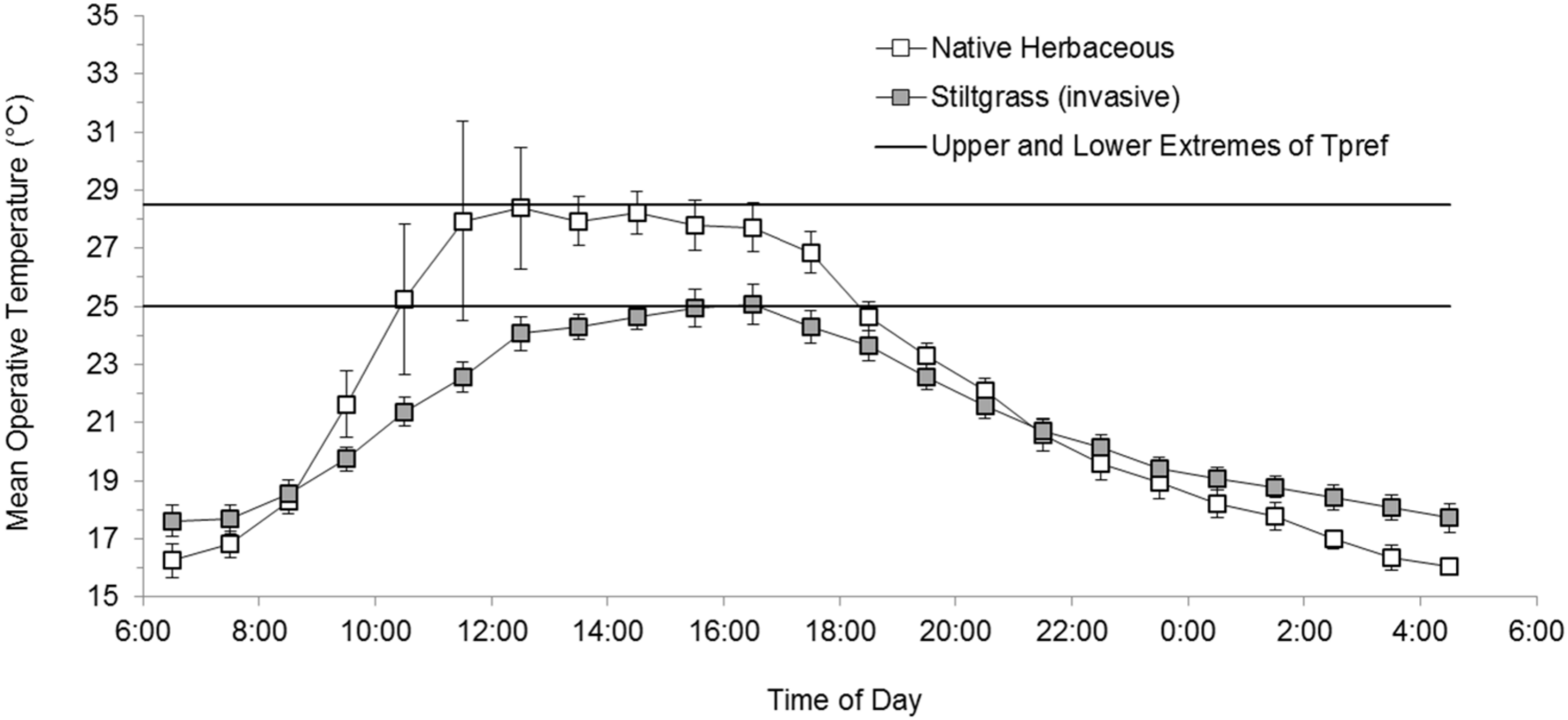

Figure 2.18. Mean daily temperatures experienced by a copperhead (operative environmental temperature) if it selected native herbaceous (open squares) or comparable stiltgrass-dominated (gray squares) habitats during the month of June.

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CHAPTER THREE

REDUCING THE POTENTIAL FOR HUMAN-SNAKE ENCOUNTERS IN A RECREATIONAL PARK

Introduction

Losos *et al.* (1995) suggest that outdoor recreation is the second leading cause for the decline of federally threatened and endangered species on public lands. On the other hand, outdoor recreation provides a means to educate and increase public awareness of conservation issues, stimulate an appreciation of wildlife through opportunities to interact with nature, and generate revenue that may be applied to conservation management. Therefore, many park managers may face difficult decisions regarding the balance of outdoor recreation with the protection of local fauna.

Additional dilemmas can arise for park managers when recreation occurs in areas shared with wildlife perceived by humans to be dangerous. While the perceived danger may be exaggerated or misinterpreted in some cases, legitimate risk for visitors (of bites, attacks, etc.) may indeed be present in others. If visitors are harmed, managers can face difficult decisions as these encounters often lead to waves of negative publicity and/or temporary closures (Gore *et al*., 2005). As a consequence, some visitors may be discouraged from enjoying the outdoors, and parks may face periods of decreased revenue. Negative consequences may exist for wildlife as well if they are persecuted, killed, or selectively removed, the last of which has questionable efficacy in preventing future encounters (Stahl *et al.*, 2001). Even when encounters are non-threatening to humans, persecution of wildlife may introduce a risk for both humans and wildlife that would otherwise not exist as many animal attacks/bites, particularly snake bites, are the result of provocation (Ernst and Zug, 1996; Loe and Roskaft, 2004; White and Gehrt, 2009).

Despite these potential complications, recreation areas may sometimes inadvertently increase the potential for human-wildlife encounters. In temperate areas, for example, artificial forest gaps are often created for recreational use in the form of hiking trails, overlooks, campsites, and picnic areas. These sites can provide an easy food source for many forms of wildlife, and artificial gaps of any kind may become important thermoregulatory sites for ectotherms such as snakes and lizards (*e.g.*, Vitt *et al.*, 1998; Greenberg, 2001; Pringle et al., 2003). Risk for wildlife is increased when aggregations occur, and this risk may be especially high when populations are small and aggregations occur in close proximity to human activities.

Herein I describe a case study where artificial forest gaps present potential management concerns for both humans and Northern Copperheads (*Agkistrodon contortrix mokasen*) in a recreational park in southern Indiana. The potential for human-Northern Copperhead encounters is described and the effectiveness of different simulated methods for reducing encounters is tested.

Methods

This study was conducted from April – October 2009 in a 573 hectare recreational park in southern Indiana. The park is characterized by a matrix of talus slopes and shallow canyons, primary and secondary deciduous upland, and several public-use areas—including frequently used hiking trails—interspersed throughout.

I captured Northern Copperheads in suitable habitat by active search from late April to late May and selected a subset of all snakes captured for surgical implantation of radiotransmitters (Holohil model SB-2T) based on size (transmitter not to exceed 2.5% of snake mass) and sex (equal proportion of males, gravid females, and nongravid females). Surgical procedures were adapted from Reinert and Cundall (1982). Isoflurane was utilized, and transmitters were placed within the coelom with antennas positioned subcutaneously.

Each snake was located approximately 3 times per week beginning after spring emergence and ending shortly after return to hibernacula in the fall. Latitude and longitude coordinates were recorded and mapped in ArcMap 9.3 (ESRI, 2009).

I defined the potential for a human-snake encounter to occur if a Copperhead was located within three meters of a recreational trail or human-use site. I considered human-use sites to be human-altered forest gaps designed and maintained by park staff for recreational purposes. I assumed that all sites received equal volumes of human traffic. Two gaps within the study area fit these criteria, which I term the “tower” and “overlook.” The tower consists of a 220 m^2 clearing surrounding a popular observation tower. It is situated at the southern extremity of a roughly north-south running ridge and receives intense sun exposure throughout the day. The entire area is regularly padded with gravel, and both the center (directly below the tower) and periphery contain light weed growth. The overlook consists of section of trail that passes over an old rock foundation (area 100 m^2), which is situated on the same north-south oriented ridge as the tower. The foundation, which has primarily a western exposure, is approximately 1.5 meters tall and 5 meters long with overlapping limestone rocks that form several crevices used by Copperheads.

To demonstrate nonrandom use of recreational sites, I generated an equal number of random locations as snake locations using ArcMap and compared the proportion of snake locations and random locations falling within three meters of a trail or artificial forest gap. I then simulated the closure of each of these sites to human-traffic in which snake locations within these sites would be greater than 3 meters from human access. I compared the proportion of snake locations within three meters of a recreational trail or artificial forest gap before and after four separate treatments: (1) no human-restricted access to the tower and overlook sites, (2) restricted access to the tower only, (3) restricted access to the overlook only, and (4) restricted access to both the overlook and the tower combined.

Comparisons between treatments were carried out through the use of multiple Chi-Square analysis. I minimized type I errors for multiple tests by adjusting the p-value level of significance through Bonferroni corrections. I considered tests to be significant if the p-value was less than the new adjusted α_{adj}, p = 0.008. I selected Chi-Square analysis as opposed to other statistical tests better suited to habitat use, because I was concerned only with the probability of a human-encounter with a snake rather than the probability of a snake selecting a particular habitat type.

Results

I obtained a total of 394 locations from 11 snakes from May – October 2009. Copperheads were significantly more likely to occur within the vicinity recreation sites (χ^2=143.05, df =1, $P < 0.001$) as 43 % of snake locations were within three meters of a trail or artificial forest gap whereas only two percent of random points were located within three meters of a trail or artificial forest gap (Fig. 3.1). As expected, not restricting access to both artificial forest gaps resulted in the highest potential for human-Copperhead encounters (Fig. 3.1) and was significantly greater than all other treatments (tower restriction: $\chi^2 = 8.48$, df = 1, $P = 0.004$; overlook restriction: $\chi^2 = 41.46$, df = 1, $P < 0.001$; tower / overlook restriction: χ^2=105.48, df =1, $P < 0.0001$). Restricting access to both the overlook and the area surrounding the tower resulted in significantly less potential for human-snake encounters when compared to restricting access to only the overlook ($\chi^2 = 21.80$, df = 1, $P < 0.001$) or the tower ($\chi^2 = 61.33$, df = 1, $P < 0.001$). When having the option of restricting access to only one recreational site, closing the overlook would result in the lowest potential for human-snake encounters ($\chi^2 = 13.23$, df = 1, $P < 0.001$).

Seven of the eleven telemetered copperheads utilized the overlook during 2009, and five of eleven utilized the tower during 2009. I also recorded an additional three unmarked copperheads at the overlook and one unmarked copperhead at the tower during 2009. During the active season (May – October), no less than three telemetered copperheads were observed at the overlook at any time, and no less than two telemetered copperheads were observed at the tower at any one time.

Discussion

Copperheads, like many ectotherms, are known to utilize forest gaps (Fitch, 1960; Reinert, 1984; Smith *et al.*, 2009; Chapters One, Two, and Four) likely as a means to thermoregulate, and, within the park, copperheads utilize canopy gaps near public access (43% of locations). This is likely due to the fact that these gaps are maintained whereas gaps in the forest interior are absent or facing successional growth, owing largely to extensive exotic plant invasions (Chapter Two). Recreational use of artificial gaps presents a potential risk for both visitors and Copperheads. For example, hikers are regularly observed hanging their legs over the edge of the overlook in close contact with crevices containing refuging or basking Copperheads, and adult and neonate Copperheads have been intentionally killed at each of these sites on multiple occasions (Dick Davis—Park Naturalist, pers. comm.).

The potential for human-Copperhead encounters could be reduced significantly by closing either or both artificial gaps in this study. Restricting access to the tower, overlook, or both would reduce encounters by 1.5, 3, or 10 x, respectively. While restricting access to both sites would provide the most substantial reduction in the potential for human-snake encounters, it may not be feasible for a park to implement multiple restrictions, and restricting access to either of the sites alone would still significantly reduce the potential for encounters.

In areas where sections of trail create gaps being utilized by wildlife, a trail itself may be moved rather than restricting access to entire areas. This can be effective when moving a trail by only a few meters. For example, the section of trail running through the overlook was moved three meters to the downhill edge of the ridge, effectively bypassing the overlook by traversing through habitat less preferable to Copperheads. This scenario may be a highly desirable alternative for park managers and visitors as visitors may still enjoy the scenic value that the artificial gap offers without encroaching on wildlife and/or disturbing important habitat. This method has been gaining endorsement from several nature preserves in Indiana, where human contact with nature is not permitted but observation is encouraged.

An alternative management practice to restriction at recreational forest gaps might involve creating additional artificial gaps in the forest interior away from public access. The creation of artificial forest gaps in the forest interior would provide increased thermoregulatory opportunities for ectotherms (Vitt *et al.*, 1998; Pringle *et al.*, 2003; Webb *et al.*, 2005) and may decrease the potential for human-wildlife encounters by providing habitat away from human access. These situations also present opportunities for vital conservation research as the degree to which different species respond to such habitat manipulation and its long term implications are largely unknown (Shoemaker *et. al*, 2009).

The selection of sites for the creation of artificial forest gaps should involve a thorough consideration of the habitat needs of any species involved. Important factors may include a number of habitat characteristics, including direction of sun exposure, slope, substrate and soil composition, understory vegetation, and geochemical habitat characteristics among countless others. For instance, Pringle *et al*. found that incident radiation was influenced predominantly by the location of canopy gaps in relation to the path of the sun; thus, the imperiled Broad-headed Snake (*Hoplocephalus bungaroides*) was restricted to canopy openings at the tops west-facing cliffs (2003). Accordingly, Northern Copperheads and many temperate reptiles are widely believed to utilize gaps on or near south-facing slopes when these habitats are available; however, such assumptions for individual populations do not always hold true for Northern Copperheads in southern Indiana (Carter and Eads, unpublished data). In the current population example, Northern Copperheads show preference for gaps on west-facing slopes; however, preference differs slightly between sex, gravidity, and season (see previous chapters). Thus, I would suggest that, at least for the current study population, artificial gaps be created in a number of situations to accommodate these differences and attempt to maximize their effectiveness (*i.e.*, use by snakes).

Even when additional artificial gaps are created or suitable habitat exists elsewhere, wildlife may continue to utilize a site—particularly if breeding or foraging success was previously high in that location (Switzer, 1997; Hass, 1998; Porneluzi, 2003). Both the tower and the overlook serve as major gestation and parturition sites for copperheads— evident from the fact that nearly all telemetered gravid females and several non-telemetered individuals selected one of these locations as their primary gestation site (only snakes in the northern subpopulation did not), and parturition has taken place at each of these sites during every year of a four-year study (see previous chapters). Unfortunately, restricting access to any recreational site will typically translate into a site no longer being managed. A paradoxical situation may exist in that it is human use that maintains low levels of vegetation or other preferred characteristics, thereby creating the attractive habitat for wildlife in the first place. If sites are not managed after restriction, wildlife may continue to utilize an increasingly lower quality habitat. Populations can also be highly vulnerable when aggregations occur in relatively few and small areas, and this risk can be greatly increased when the individuals using those sites are primarily pregnant females for example. Even greater risk may be present when those habitats are also subject to successional change or anthropogenic perturbations (*e.g.*, Packer, 1986; Hutchings, 1996; Sadovy and Domeier, 2005; Vepsalainen *et al*., 2007). Considering these potential management concerns, particular care should be taken in determining the proper course of action when aggregations occur. I recommend that low-impact management (*i.e.*, intermittent hand removal of vegetation) continue where possible at least until there is evidence that wildlife have transitioned into other habitats of equal or higher quality.

Overall, the decision to restrict human access to any site should first take into account its overall expected effectiveness in protecting wildlife and recreationists and its impact on recreational opportunities. A better understanding of how different species respond to restrictions under varying scenarios as well as the resulting changes in habitat will likely offer insight into better managing these habitats for vulnerable populations.

Note: After the results of this study were reported to the Indiana Department of Natural Resources, the overlook and tower sites were closed to park visitors. A permanent bypass trail was created on the east-facing, downhill, side of the overlook, and the gravel pad around the base of the tower was no longer manicured (although the trail leading to tower steps was not closed for obvious reasons). Each site quickly became overgrown with exotic vegetation, which research volunteers and I made an effort to control during the first year of closure. However, the Indiana Division of Nature Preserves volunteered in late 2010 to manage each of these sites for copperheads and other wildlife on a permanent basis. Both sites continue to be important gestation and basking sites for multiple snake species, and there has been no sign of decreased use by copperheads.

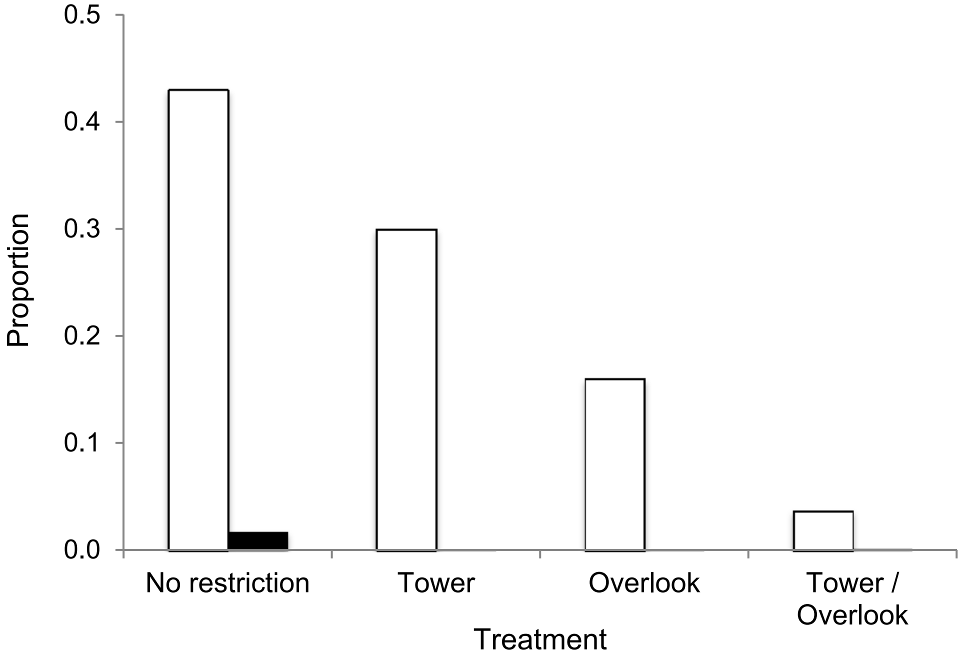

Figure 3.1. The potential for a human-Northern Copperhead encounter. The proportion of snake locations (n=11 snakes) within three meters of a recreational trail or artificial forest gap during each of four separate treatments: no restricted access, restricted access to tower only, restricted access to overlook only, and restricted access to both the tower and overlook. White bars represent snake locations and black bars represent random locations. The proportion of random locations within three meters of the tower, overlook, and tower/overlook are all < 0.01.

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CHAPTER FOUR

MANAGED HABITATS AS ECOLOGICAL TRAPS IN AN EXOTIC PLANT-INVADED LANDSCAPE

Introduction

In any property where public use is anticipated and welcomed, general maintenance operations are conducted with the intent to make areas accessible or safer to recreational users, maintain structural integrity (*e.g.*, of roadsides and levees), or simply to make views more attractive. Mowing and clearing roads and trails of debris and fallen timber are probably the most common maintenance activities. In many cases, grassy fields and perimeters are targeted to control woody vegetation. This type of periodic mowing can inadvertently create habitats that are favored by early successional species such as some reptiles, birds, and small mammals (Foster and Gaines, 1991; Askins, 1993; Fox *et al.*, 2003; Bailey *et al.*, 2011). In addition, fallen timber and debris that are moved to designated areas often accumulate to form brush piles that may be favored by many animals either as refuge sites or foraging areas (Beer, 1961; Gehrt and Fritzell, 1999, Sperry and Weatherhead, 2010).

Many maintenance scenarios have the potential to create what may be termed an ecological trap, where an animal is attracted to, and preferentially utilizes, an area that is actually relatively lower in quality than other accessible habitats (Gates and Gysel, 1978). Ecological traps resulting from human-mediated habitat alterations are typically based on subtle mechanisms that affect breeding or nesting success (*e.g.*, Chasko and Gates, 1982; Best, 1986; Kershner and Bollinger, 1996; Flaspohler, 2001; Kolbe and Jansen, 2002; Hawlena *et al.*, 2010). However, ecological traps can also result from more direct human impacts such as hunting (Delibes *et al.*, 2001; Battin, 2004; Marinez-Abrain *et al.*, 2007). The occurrence of ecological traps of any kind can have significant implications for conservation and natural resource management (Battin, 2004), especially when they are the result of activities carried out by the parks or refuges that are attempting to conserve biodiversity.

Strategies for general property management and natural resource management can be conflicting, but often interwoven, aspects of daily operations within protected lands that are set aside with public use as a primary intended function. State and federal parks fall under this type of land use strategy where lands are often managed for public use while attempting to minimize any potential impacts on local flora and fauna (Lemons, 1987). It can be difficult for land managers to accomplish such objectives without first having a detailed knowledge and understanding of the local ecology. It can also be impractical to cease or alter particular operations that are necessary for the general function of a park. Therefore, balancing property management with natural resource management can be a difficult task—one type of approach must often yield to the other and often without a thorough understanding of the consequences resulting from these decisions.

Land managers may be presented with more difficult decisions when conflicting objectives occur within natural resource management itself. Many natural areas are burdened by the introduction and proliferation of nonnative invasive plants, and, in large infestations, it is often necessary to employ repeated mechanical means of exotic plant removal such as brush-hogging (USFWS, 2009). In areas where natural habitat is extremely limited, sites undergoing restoration may represent newly available, attractive habitat for some wildlife. If wildlife are attracted to these sites, and management operations occur repeatedly at times when wildlife are present, these sites may become ecological traps.

I investigated the potential occurrence of ecological traps for Northern Copperheads (*Agkistrodon contortrix mokasen*) as a result of property management and restoration activities in a state-owned park in southern Indiana. Copperheads were monitored by radiotelemetry during a larger-scale investigation into nonnative invasive plant impacts on thermoregulation, which took place from June 2008 – October 2011. Toward the end of the 2008 field season, the park began management operations that aim to control invasive plants. Efforts thus far have relied primarily on mechanical means of vegetation removal in conjunction with herbicide application from off-road vehicles. The majority of managed sites occur within the known range of copperheads within the park, and there is no indication that the particular locations where management took place had been of previous interest to copperheads (Richard Davis, Indiana Department of Natural Resources, pers. Comm.).

In order to demonstrate the existence of an ecological trap, Robertson and Hutto suggest that three criteria must be met (2006). These include equal or greater preference for one habitat over another, a ‘reasonable measure’ of differential individual fitness among habitats, and reduced individual fitness within a preferred habitat relative to other available habitats. In addition to these criteria, two types of ecological traps have been proposed based on habitat preference, including ‘equal-preference traps’ and ‘severe traps.’ There are relatively few published examples of ecological traps that demonstrate each of these criteria (Robertson and Hutto, 2006).

My objectives herein are thus to (1) demonstrate the level of Northern Copperhead preference for managed areas, (2) illustrate direct impacts of management activities on Northern Copperheads, (3) demonstrate differential fitness in individuals selecting managed habitats by using mortality and injury as surrogate measures, and (4) provide management recommendations that aim to reduce impacts on native wildlife with minimal influences on management objectives.

Methods

Study Site

This study was conducted at a 570-hectare state-owned park in southern Indiana from June 2008 – October 2011. The park occurs in the Muscatatuck Flats and Canyons region of southern Indiana. It is characterized by mixed deciduous upland and several talus slopes and rocky ravines with public use sites and hiking trails interspersed throughout. It is bordered on the south by the Ohio River and is essentially an island of semi-natural habitat within a broader suburban landscape. There are currently over 30 exotic plant species that have become naturalized in the park (Carter and Kingsbury, personal observations), the majority of which are listed as the ‘most unwanted’ plant pests in the state of Indiana (CAPS, 2009). Management operations by park staff are targeting primarily exotic shrub and herbaceous species within the vicinity of public use and within the known range of copperheads in the park. There are currently five primary areas where management is taking place (Fig. 4.1).

Radiotelemetry

I captured Northern Copperheads opportunistically throughout each season with the majority of captures occurring in April and May. Each snake was outfitted with temperature sensitive Holohil model SB-2T transmitters (Holohil Systems Ltd., Carp, Ontario) following surgical procedures adapted from Reinert and Cundall (1982) and using isoflurane as an anesthetic. Effort was made to outfit an equal proportion of adult males, nongravid females, and gravid females, and the 5 gram transmitter never exceeded 2.5% of a snake's body mass. Snakes were outfitted within two days of capture and released within one week of their initial capture date.

Each snake was located an average of three times per week during the active season (early May – October) using a handheld telemetry receiver. Latitude and longitude coordinates were recorded with a handheld GPS, and notes were taken on the health and state of each individual snake as well as the circumstances surrounding any mortality or injury.

Habitat Preference

Available habitats and snake locations were mapped in ArcMap 10 (ESRI, 2010) using aerial photographs and were systematically confirmed by on-site surveys during the 2009 and 2011 field seasons. Habitats were delineated based on vegetation structure and level of human and natural disturbance, leading to the following habitat categories: forest, natural forest gap, hiking trail, managed gap, residential, road, and agricultural (Fig. 4.1). Forest represented areas that were not subject to noticeable direct human or natural disturbance and could be broadly characterized as upland forest. Natural gaps included habitats characterized by low or absent canopy cover and low woody vegetation due to previous natural disturbance such as windfall and/or washouts (unmanaged grasslands do not occur within the study site). These sites were qualitatively distinguished from all other sites except forest by lack of direct human disturbance. A managed gap was defined as a natural area subject to periodic maintenance (*i.e.*, altered through mechanical means once or twice per year) but otherwise lacking human-disturbance. Sites included areas brush-hogged to control exotic shrubs, margins of human-use sites that were mowed and treated with herbicide periodically to control exotic herbaceous cover and woody vegetation, as well as forest clearings where clippings and debris were discarded and occasionally manipulated and compacted. Consistent among all managed gaps were low or absent canopy closure and low woody understory vegetation as well as the occurrence of occasional mechanical alterations. Hiking trails were included as a distinct habitat as they represent continual, passive disturbance in a semi-natural state, effectively excluding them from any other category.

I calculated the proportion of locations in each habitat for each individual snake and then determined the proportion of available habitats using 2000 random locations generated within the study site using ArcMap. All snake locations were confirmed to occur within a particular habitat by reviewing field-collected data, which included a categorical variable for macrohabitat. I considered females to represent two separate individuals between reproductive years due to significant differences in habitat use between reproductive states (see previous chapters). A snake was included in the analysis only if it was monitored for one full activity season.

To determine habitat preference at both the landscape (within the range of all telemetered snakes) and home range level (within the activity range of each individual snake), I utilized the Bycomp extension (Ott and Hovey, 1997) in SAS 9.2 (SAS Institute, Cary, NC). Bycomp performs a compositional analysis as described by Aebischer *et al.* (1993), comparing log-ratio proportions of used habitats to available habitats through multivariate analysis of variance (MANOVA). In the event that nonrandom habitat use is detected, Bycomp uses *t*-tests to make pairwise comparisons between habitats. A table of randomized p-values and *t*-statistics then provides a basis for ranking each habitat in order of preference.

Habitat-Specific Fitness

For analyses of habitat-related fitness costs, I combined nonfatal injury and mortality events into one category I termed “injured.” Injury was defined as evisceration, visible lacerations or puncture wounds extensive enough to expose visceral tissue, and/or broken bones (determined by palpation). I used a Fisher’s exact test of independence to determine if a relationship existed between injury and use of managed areas by comparing the frequency of injured snakes using managed versus unmanaged sites. Snakes that were never recovered due to faulty transmitters or other unknown factors were considered censored and eliminated from the analysis. To avoid pseudoreplication, I included only one event for any individual in the analysis (including for females between reproductive states). This was appropriate given that snakes exhibited high site fidelity throughout the duration of the four-year study (Carter and Kingsbury, *personal observation*)—potentially making them prone to repeated injuries under the hypothesis that injury was not independent of the habitat selected.

Results

Radiotelemetry

Twenty-two Northern Copperheads, consisting of 12 females and 10 males, were tracked between June 2008 and October 2011. Four females were tracked during both gravid and nongravid years, and three snakes were tracked fewer than 15 times, giving an effective sample size of 23 snakes (7 gravid females, 7 nongravid females, and 9 males) for macrohabitat preference analysis.

Habitat Preference

Because of low use by snakes and limited availability of residential, road, and agricultural, these habitats were combined into one category termed anthropogenic, representing continuous human impact in a completely unnatural state. Forest constituted the vast majority of habitat available to snakes within the study area at 74.95% of total composition. This was followed in order of decreasing availability by anthropogenic at 17.50%, managed gap at 3.60%, trail at 2.70%, and finally natural gap at 1.25% (Table 4.1). At the landscape level, compositional analysis ranked habitats in the following order of preference: managed gap>natural gap>>>trail>>>undisturbed forest>>>anthropogenic; with >>> indicating a significant difference (Fig. 4.2). Within individual home ranges, habitats were ranked as natural gap>>>managed gap>>>trail>anthropogenic>undisturbed forest (Fig. 4.2). Preference for managed and natural gaps was consistent between years at both the home range and landscape level.

Habitat-Specific Fitness

Sixteen out of the 22 telemetered copperheads (72.7%) suffered injury (fatal and nonfatal combined) during the course of this study, with 12 (54.5%) as a result of management operations (Fig. 4.3). Eight copperheads (36.4%) suffered fatal injury as a result of management operations, whereas three suffered predation (13.6%), and one was intentionally killed by a visitor (4.5%). All nonfatal injuries (18.2%) were the result of management operations, with several snakes suffering repeated injuries (not included in analyses) as a result of management operations (Fig. 4.3). Of those fatal injuries that were a result of management operations, three were the result of being crushed during mowing or brush cutting operations, three were crushed in a brush pile being manipulated by heavy machinery, and two died following heavy herbicide treatment. Nonfatal injuries included two snakes cut by mowers and two crushed in brush piles (Table A.5). All injuries that occurred within managed areas were due to management activities, and no injury that occurred outside of a managed area was due to management activities. Overall, snakes utilizing managed areas suffered a higher rate of injury (54.5%) than snakes utilizing only non-managed areas (18.2%), while a greater number of snakes were uninjured when utilizing only non-managed areas (27.3%) than when utilizing managed areas (0.0%). This relationship was significant ($P = 0.0028$, Fisher's exact test).

Discussion

Northern Copperheads exhibited strong and nearly equal preference for managed and natural gaps. Given that managed and natural gaps share recognizably common features, *i.e.*, low woody vegetation and lack of canopy closure, it appears likely that copperheads select each of these habitats based on the same environmental cue(s). There is strong evidence from associated studies that the environmental cue for selection of these sites is either thermal or a related cue(s) based on vegetation structure that is probably thermally driven (see: Chapter Two). Moreover, selection for forest gaps of any kind and their importance in thermoregulation and gestation by copperheads is supported by associated studies, which also reveal equivalent behavioral use and selection at the microhabitat scale within these two habitats (see: Chapters One and Two).

Results from telemetered copperheads indicate that costs were greater in managed areas relative to all other available habitats. The measure of differential fitness used herein consisted of both mortality and nonfatal injury. Mortality represents an immediate and obvious fitness loss. Unfortunately, the low number of *nonfatally*-injured snakes did not afford us the ability to statistically compare measures of fitness between nonfatally-injured snakes and uninjured snakes. However, there is considerable evidence that reproduction in pit-vipers is facultative and largely dependent on energy stores and resource availability (reviewed in Holycross and Goldberg, 2001). As any injured animal must allocate energy to healing that could otherwise be allocated to mate searching and/or gametogenesis (Derickson, 1976), there is potential for fitness loss due to nonfatal injury. Moreover, female copperheads at in southern Indiana reproduce consistently on a biennial cycle while males exhibit courtship and copulation with multiple females per year (personal observations, see Chapter One). This appears to be the case with copperhead populations throughout the species' geographic range (Fitch, 1960; Minton, 2001; Ernst, 2011). Reduced reproduction and breeding behavior was observed only in individuals following nonfatal injuries, which included lack of courtship or other breeding behavior by males and failure by females to produce young on a biennial cycle despite having been copulated by multiple males during the previous breeding season. Thus, I feel there is sufficient evidence for reduced fitness in nonfatally injured snakes in order to include nonfatal injury alongside mortality in the analysis as a measure of differential fitness.

Disconcertingly, there is evidence to suggest that losses due to management were substantially larger than has been quantitatively demonstrated. Five *non*-telemetered copperheads were collected as road mortalities during the course of the study, whereas only two *non*-telemetered snakes were confirmed to suffer mortality as a result of management activities. Furthermore, no telemetered snake suffered injury as a result of vehicle collision despite several snakes crossing roads multiple times and most snakes selecting habitat in close proximity to roads during each year of the four-year study. If the sample is considered to be representative of the total population during this period of time, it is probable that far more snakes were killed or nonfatally injured as a result of management operations were actually detected.

This creates a potential dilemma for land managers. The criteria used to quantify the success of restoration and management have long been controversial, especially when considering narrow versus broad-scale management strategies (*e.g.*, single species versus eco-system management; see: Simberloff, 1998; Ruiz-Jaen and Aide, 2005; Simberloff, 2008). Under a broad-scale management strategy, negative impacts on one or relatively few species may not warrant adjustments to management methods. However, if obvious mechanistic causes for a species or population decline have been detected, and mitigation is neither difficult to perceive nor costly, there may be little rationale for not acting (Simberloff, 1998; Simberloff, 2008). Moreover, it is unlikely that copperheads are the only form of wildlife negatively impacted by the management operations described herein. Indeed, mowing has been identified as a factor resulting in mortality in snakes—including imperiled Eastern Massasaugas (*Sistrurus catenatus catenatus*) (Durbian, 2006), turtles—including imperiled Wood Turtles (*Glyptemys insculpta*) (Saumure *et al*., 2006), and ground-nesting birds (Vickery *et al*., 2006).

From a thermoregulation perspective, there remains potential for reduced fitness if invasive plants are not managed and habitats not reclaimed. While forest gaps offer high thermal quality for both basking individuals and gestating females, thermoregulatory opportunities within the forest interior are severely limited due to high densities of nonnative invasive plants. This is especially true of exotic shrub monocultures wherein operative temperatures are consistently below the preferred body temperature range of copperheads (see Chapter Two). What is not known from the current study or associated studies is whether fitness costs are greater from exotic plant limitations on thermoregulation (discussed in Chapter Two) or from the direct injury or mortality that results from selecting managed habitats. Anecdotal evidence indicates a steady population decline and reduction in range for copperheads (and other species) within the park since the introduction and proliferation of several exotic plant species beginning in the early 1980's (Richard Davis, Indiana Department of Natural Resources, pers comm). With high densities of exotic plants eliminating forest gaps and resulting in less suitable habitat, it is likely that exotic plants have played a significant role in the presumed declines and range reductions (discussed further in: Chapter Two). Herein lie additional dilemmas for copperheads and other flora and fauna since management reclaims critical habitats that are preferentially utilized while management activities themselves appear to be the only negative effects associated with selecting these sites.

Partial resolutions exist for this Catch-22. One of the most straightforward and effective solutions may be to alter the timing of management operations in order to accommodate temporal use of particular habitats by wildlife. Controlling woody vegetation is one of the most common practices this study site and others and is usually accomplished through the use of heavy equipment such as brush mowers and tractors. The impacts of such activities can be reduced by restricting management operations to times when copperheads are not present. Fortunately, there is a clear distinction in temporal use of managed areas; copperheads utilize managed areas after a brief transitional period following spring emergence from hibernacula up to a similar brief transitional period just before return to hibernacula in the fall (see: Chapter One). Concentrating management operations outside of this activity period will reduce mortality and injury and still permit effective management operations. This approach is currently being implemented by park staff at Clifty and is applicable to any organism exhibiting seasonal variation in habitat use, which, at the very least, includes most reptiles inhabiting temperate regions (Reinert, 1993).

One dilemma arising from this suggestion is that availability of laborers is largely restricted to the summer since many are either students or are provided funds through seasonal programs, or both. In such a case, it may be useful to employ a less aggressive means of vegetation removal. Guidelines for amphibian and reptile habitat management—including vegetation removal practices to reduce impacts on native herpetofauna—are outlined in several habitat management books produced by Partners in Amphibian and Reptile Conservation (PARC) (Kingsbury and Gibson, 2012; Bailey *et al*., 2006; Mitchell *et al*., 2006). These books are excellent tools for all land managers, and some suggested practices to reduce impacts on herpetofauna include hand removal of vegetation when feasible or the use of a minimum mower deck height of 8 – 12 inches if mowing is the only feasible option. My experience with the current study leaves me inclined to press for hand removal since snakes were crushed rather than cut by heavy equipment in most cases. In circumstances where periodic mowing or hand removal is not suitable (*e.g*., rapidly-growing species and exotic grasses), it may be advantageous to maintain a continuously low height (maintained as ‘lawn’) in which most wildlife are less likely to seek refuge.

Several snakes were killed or nonfatally injured when utilizing brush piles or the taller herbaceous areas immediately adjacent to brush piles within managed gaps. As brush piles are a known attractant even outside of the summer activity season for reptiles (Pitman and Dorcus, 2009; Sperry and Weatherhead, 2010), amphibians (Rittenhouse, 2008;), birds (Miller, 2010), and mammals (Kotler *et al*., 1992; Gehrt and Fritzell, 1999), I recommend they only be constructed adjacent to or within natural areas if they are quickly compacted or otherwise disposed of, or if there is no intention of future use or manipulation.

By and large, evidence from this study indicates that managed areas serve, at a minimum, as equal-preference traps for Northern Copperheads. Both managed and natural gaps are preferred by copperheads, while use of managed habitats results in greater probability of reduced fitness. The costs to an individual snake associated with selecting a managed site are high, but the costs associated with selecting some unmanaged habitats other than natural gaps may be equally high. The primary purpose of the management activities described herein is the control of nonnative invasive plants, leaving multiple dilemmas for both land managers and wildlife. A better understanding of the impacts of habitat manipulation and exotic plants will be valuable for multiple forms of wildlife, but effective long-term resolutions for any species will likely involve simple adjustments in the timing and methodology of vegetation control and other habitat manipulations.

Despite the negative consequences associated with management and restoration, additional positive and promising corollaries do exist. Determining important habitat parameters that attract wildlife can be a difficult task, which is evidenced by the varying success of predictive habitat models (see: Felding and Haworth, 1995; Fielding and Bell, 1997; Guisan and Zimmerman, 2000). There is often no way of knowing how, when, or if wildlife will respond to habitat manipulations or restoration efforts (Scott *et al*., 2001; Miller and Hobbs, 2007; Shoemaker *et al*., 2009). The current knowledge regarding long-term response by wildlife—particularly by snakes—to targeted habitat manipulation is extremely limited (Shoemaker *et al*., 2009). However, this study provides evidence that habitat manipulation and restoration of forest gaps can elicit a positive and enduring response within a relatively short time. Copperheads at Clifty were not known to utilize managed areas before these habitats were manipulated to remove woody vegetation. Based on data from associated studies, managed habitats appear to represent newly available basking areas and gestation sites owing to their high thermal quality and related vegetation structure (Chapters Two and Three). While snakes suffered significant fitness losses in managed habitats, preference for managed gaps did not change significantly throughout the duration of the study while intensity of use of managed gaps appeared to followed an upward trend (along with intensity of management efforts and rate of injury) (Fig. 4). If future management strategies incorporate methods to reduce management-related losses (*e.g*., by altering the timing of management efforts), it is probable that restoration efforts will ultimately benefit copperheads. Thus, this study offers a promising lead in the study of habitat manipulation and restoration efforts for wildlife management purposes.

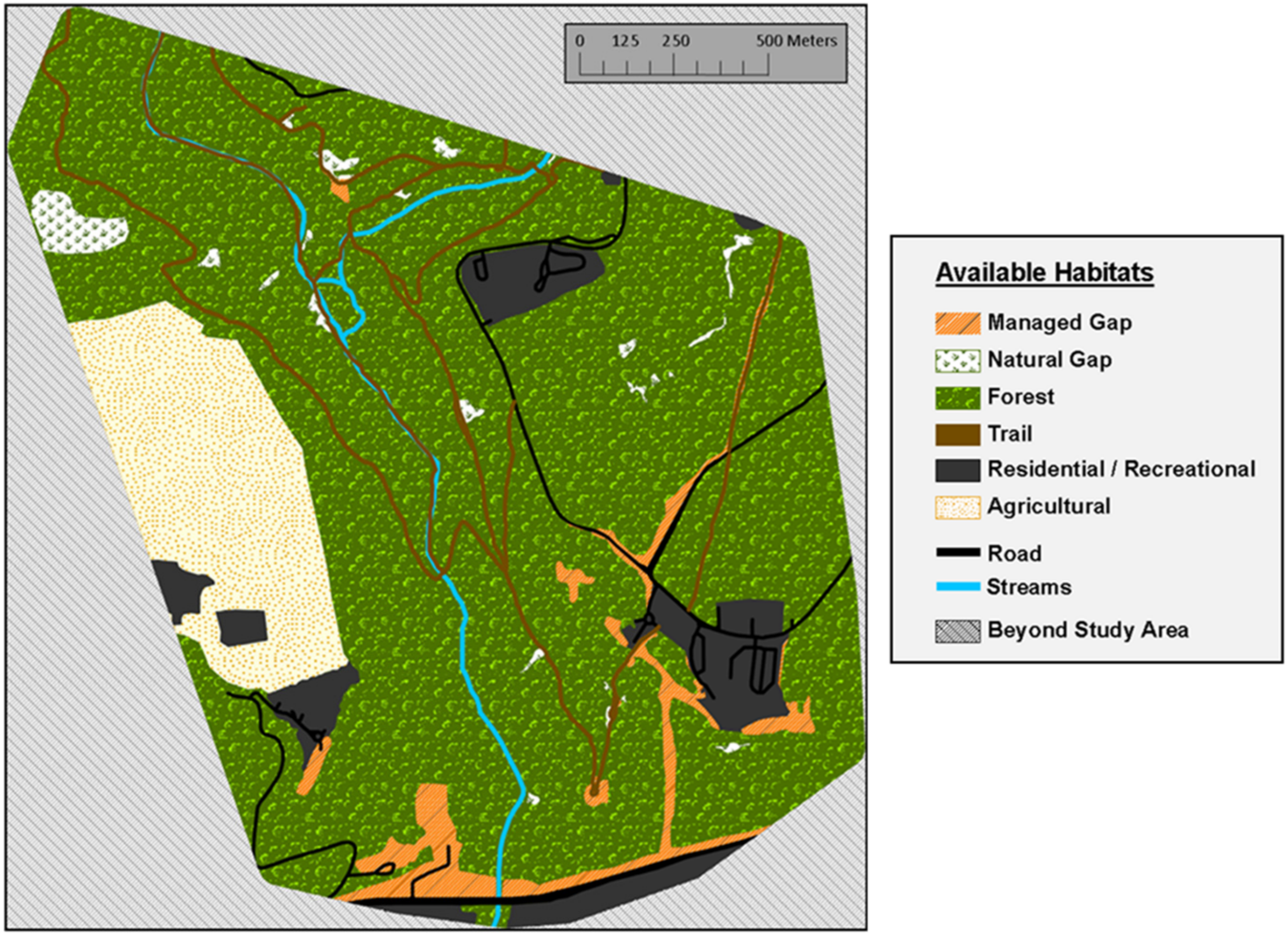

Figure 4.1. Habitats available to telemetered copperheads. Habitats were delineated using aerial photographs and ground-truthing in 2009 and 2011. Study area is defined by a minimum convex polygon around all snake locations.

Table 4.1. Percentage of available habitats at the landscape level and mean percentage (±1 SE) of habitats available to each snake at the activity range level.

Level	Managed Gap	Natural Gap	Trail	Anthropogenic	Forest
Landscape	3.60	1.25	2.70	17.50	74.95
Activity Range	15.46 (±4.44)	1.98 (±0.45)	3.00 (±0.62)	3.80 (±1.52)	75.98 (±4.10)

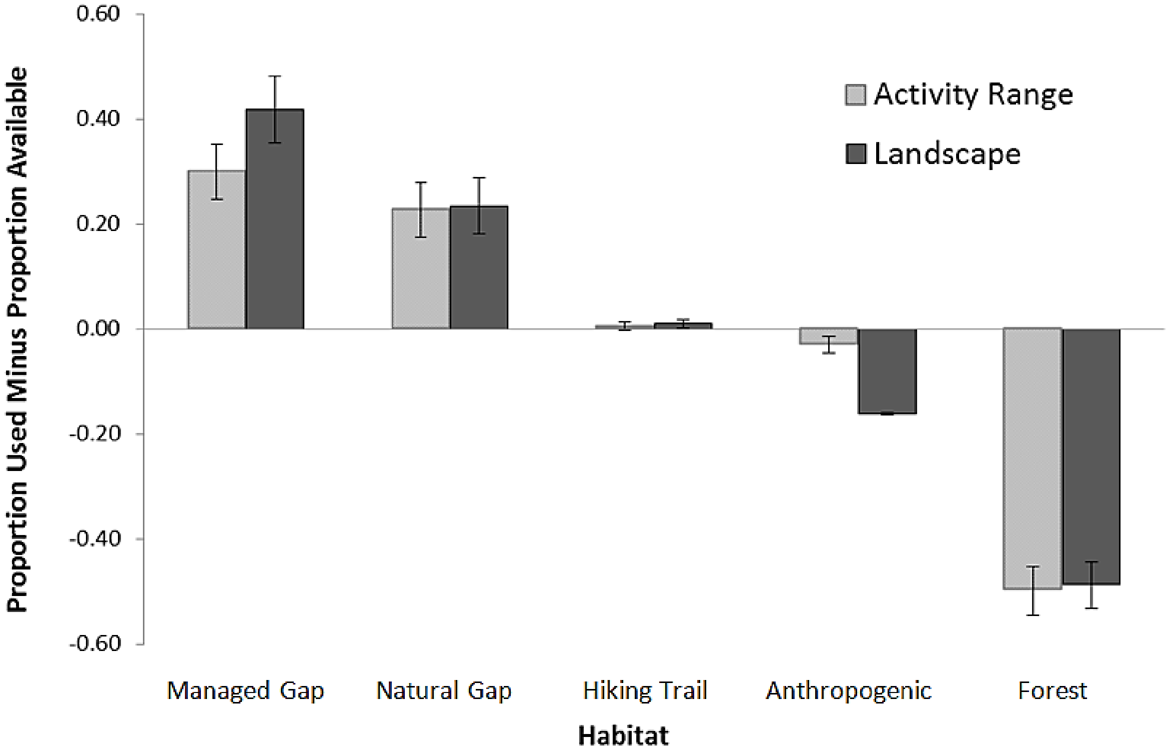

Figure 4.2. Relative use versus availability at the activity range (light bars) and landscape level (dark bars) for Northern Copperheads at Clifty Falls State Park. Error bars represent one standard error above and below the mean (*N* = 23).

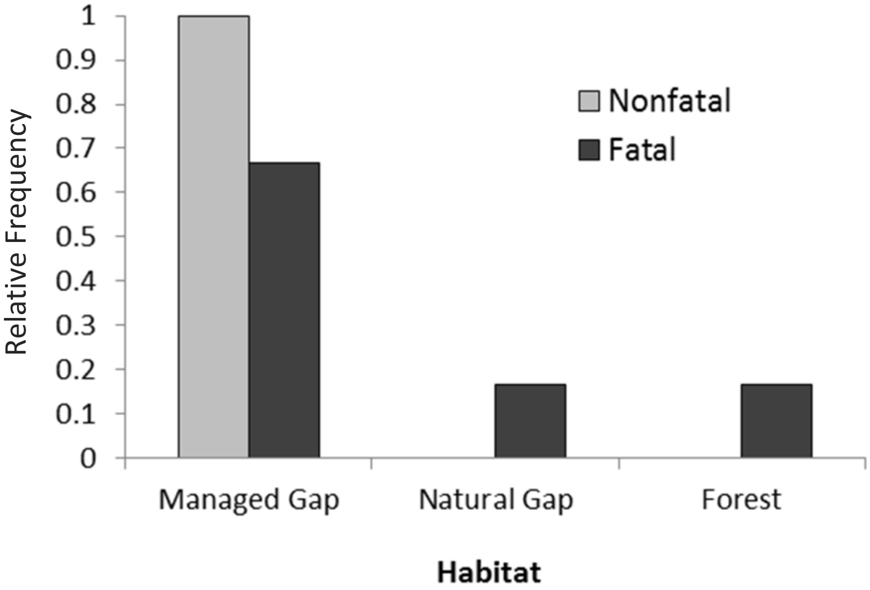

Figure 4.3. Relative frequency of nonfatal (light bars) and fatal (dark bars) injury in habitats available to telemetered Northern Copperheads over the course of the study. Graph represents 12 fatal and 4 nonfatal injuries based on individual snakes rather than actual injury events. Three snakes suffered more than one nonfatal injury, but the relative frequency in each habitat will not change if these events are included since all nonfatal injuries occurred in ‘managed gap.’ No injury occurred in ‘anthropogenic’ or ‘trail,’ thus they are not shown here.

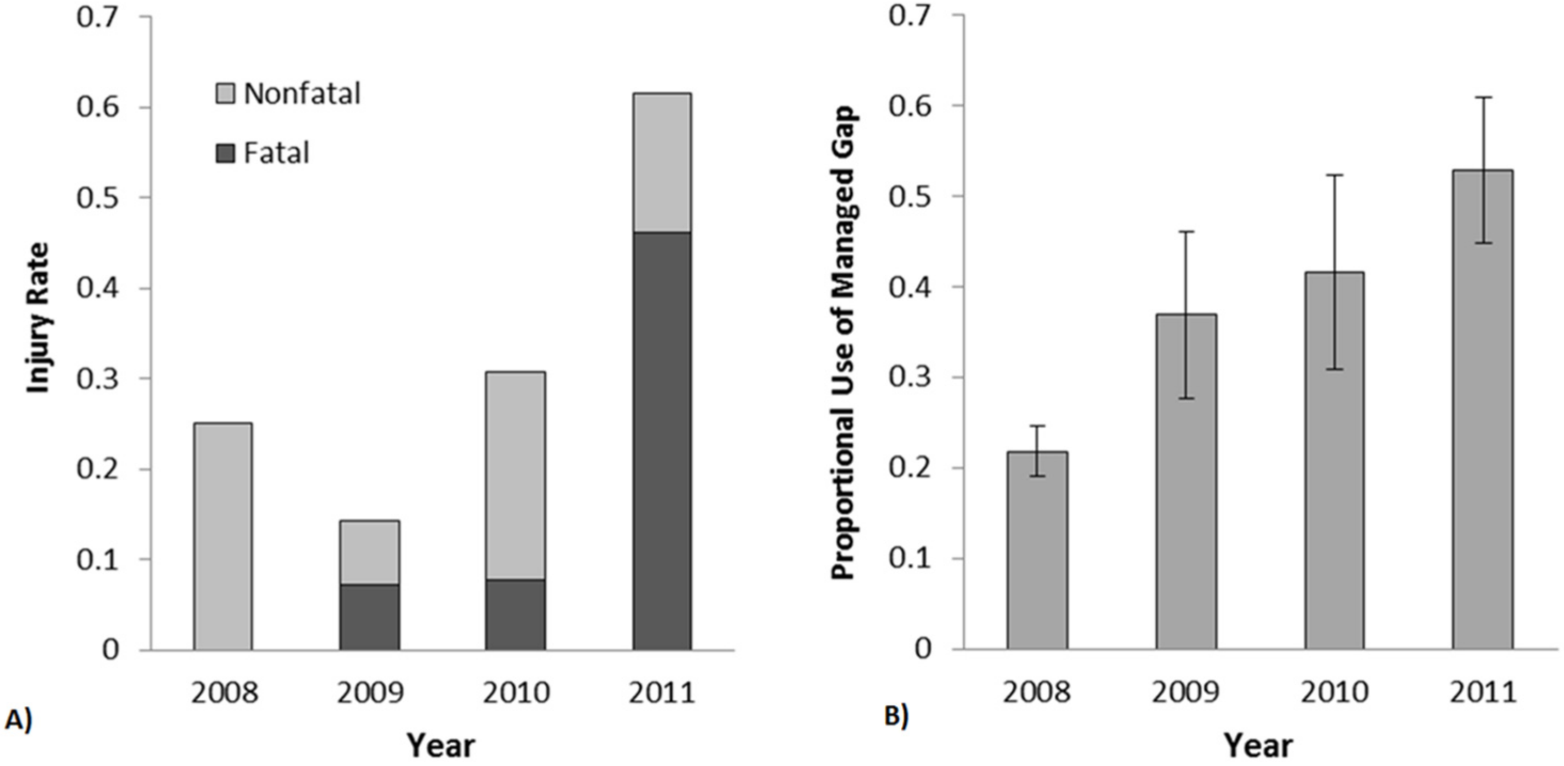

Figure 4.4. Injury and habitat use in managed gaps. (A) Rate of nonfatal (light portions) and fatal (dark portions) injury in telemetered Northern Copperheads due to management activities during each year of the study. (B) Proportional use of managed gaps by telemetered Northern Copperheads during each year of the study. Error bars represent 1 standard error above and below the mean. Sample sizes are 4 for 2008, 14 for 2009, 13 for 2010, and 13 for 2011. Some snakes were tracked for longer than one year.

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APPENDIX

APPENDIX

Table A.1. Variables recorded at snake locations and paired random locations included in analysis of Intermediate-Scale habitat selection by Northern Copperheads.

Variable	Description
canopy	percentage of overhead canopy closure, using spherical densitometer
gap	≥ 30 percent gap in canopy cover from any perspective
nat.over	distance (m) to nearest native understory tree (woody, erect growth, ≥ 7.5cm dbh)
nat.under	distance (m) to nearest native understory tree (woody, erect growth, < 7.5cm dbh)
nat.shrub	distance (m) to nearest native shrub (woody, diffuse growth)
nat.vine	distance (m) to nearest native vine (woody, climbing or creeping)
nat.herb	distance (m) to nearest native herbaceous patch (area > size of coiled snake)
ex.over	distance (m) to nearest exotic understory tree (woody, erect growth, ≥ 7.5cm dbh)
ex.under	distance (m) to nearest exotic understory tree (woody, erect growth, < 7.5cm dbh)
ex.shrub	distance (m) to nearest exotic shrub (woody, diffuse growth)
ex.vine	distance (m) to nearest exotic vine (woody, climbing or creeping)
ex.herb	distance (m) to nearest exotic herbaceous patch (area > size of coiled snake)

Table A.2. Variables included in analysis of fine-grained microhabitat selection by Northern Copperheads as recorded within one-meter diameter plots at snake and paired random locations.

Variable	Description
n.tree	density (% coverage) of native tree (foliage ≤ 1 meter from ground level)
nat.shrub	density (% coverage) of native shrub (woody, diffuse growth)
nat.vine	density (% coverage) of native vine (woody, climbing or creeping)
nat.herb	density (% coverage) of native herbaceous ground cover
ex.tree	density (% coverage) of exotic tree (foliage ≤ 1 meter from ground level)
ex.shrub	density (% coverage) of exotic shrub (woody, diffuse growth)
ex.vine	density (% coverage) of exotic vine (woody, climbing or creeping)
ex.herb	density (% coverage) of exotic herbaceous ground cover
nat.shrub.ht	modal height of native shrub (woody, diffuse growth)
nat.vine.ht	modal height of native vine (woody, climbing or creeping)
nat.herb.ht	modal height of native herbaceous ground cover
ex.shrub.ht	modal height of exotic shrub (woody, diffuse growth)
ex.vine.ht	modal height of exotic vine (woody, climbing or creeping)
ex.herb.ht	modal height of exotic herbaceous ground cover

Table A.3. Occurrence rates for exotic plant species at the macrohabitat level (60-meter diameter plots) at Clifty Falls State Park. This list is not inclusive of all exotic species present at Clifty Falls State Park—only those that were documented and mapped.

Common Name	Scientific Name	Occurrence Rate
Privet	*Ligustrum* spp	0.701
Oriental bittersweet	*Celastrus orbiculatus* Thunb.	0.589
Garlic mustard	*Allaria petiolata* (Bieb.) Cavara & Grande	0.570
Japanese honeysuckle	*Lonicera japonica* Thunb.	0.452
Multiflora rose	*Rosa multiflora* Thunb.	0.346
Autumn olive	*Eleaganus umellata* Thunb.	0.230
Tree of heaven	*Ailanthus altissima* (P. Mill.) Swingle	0.204
Japanese stiltgrass	*Microstegium vimineum* (Trin.) Camus	0.204
Bush honeysuckle(s)	*L. maackii* (Rupr.) Herder; *L.* x *bella* Zabel	0.170
Star-of-Bethlehem	*Ornithogalum umbellatum* Linneaus	0.144
Wine raspberry	*Rubus phoenicolasius* Maxim	0.099
Tall fescue	*Lolium arundinaceum* (Schreb.) Darbyshire	0.086
Armenian blackberry	*R. armeniacus* Focke	0.071
Johnson grass	*Sorghum halepense* Pers.	0.047
Jetbead	*Rhodotypos scandens* (Thunb.) Makino	0.041
Winged burning bush	*Euonymus alatus* (Thunb.) Siebold	0.028
Ground ivy	*Glechoma hederacae* Linnaeus	0.022
Common teasel	*Dipsacus sylvestris* Huds.	0.013
Canada thistle	*Cirsium arvense* (L) Scop.	0.011
Princess tree	*Paulownia tomentosa* (Thunb.) Steud.	0.011
Winter creeper	*E. fortunei* (Turcz.) Hand. –Mazz.	0.011
Crownvetch	*Coronilla varia* Linnaeus	0.009
English ivy	*Hedera helix* Linneaus	0.009
Mahaleb cherry	*Prunus mahaleb* Linnaeus	0.009
Norway maple	*Acer platanoides* Linnaeus	0.006
Periwinkle	*Vinca minor* Linnaeus	0.006
Silk Tree	*Albizia julibrissin* Durazz.	0.004
Common mullein	*Verbascum Thapsus* Linneaus	0.002
Japanese barberry	*Berberis thunbergii* D.C.	0.002
Moneywort	*Lysimachia nummularia* Linneaus	0.002
White mulberry	*Morus alba* Linneaus	0.002

Table A.4. Multivariate regression models used to predict T_e in habitats at Clifty Falls State Park. Variables in the analysis included air temperature ($\mathit{Air.temp}$), bare soil temperature ($\mathit{Soil.temp}$), solar radiation ($\mathit{Solar.rad}$), precipitation (Precip), and wind speed (Wind).

Habitat	Equation	R^2
Closed-canopy forest	$0.78\mathit{Soil.temp} + 0.225\mathit{Wind} + 1.19$	0.92
Refuge in forest	$0.72\mathit{Soil.temp} - 0.79\mathit{Solar.rad} - 1.94$	0.84
Native shrub	$0.96\mathit{Soil.temp} + 0.548\mathit{Wind} - 2.86$	0.85
Native vine	$0.88\mathit{Soil.temp} + 0.44\mathit{Wind} - 0.88$	0.91
Native herbaceous	$0.99\mathit{Soil.temp} + 0.52\mathit{Solar.rad} + 0.77\mathit{Wind} - 4.63$	0.90
Glade	$0.94\mathit{Soil.temp} + 2.87\mathit{Solar.rad} + 0.86\mathit{Wind} - 1.90$	0.70
Refuge on glade	$0.73\mathit{Soil.temp} + 0.97\mathit{Solar.rad} + 4.72$	0.74
Privet	$0.75\mathit{Air.temp} - 1.03\mathit{Solar.rad} - 0.65\mathit{Wind} + 5.20$	0.88
Autumn olive	$0.78\mathit{Soil.temp} - 0.25\mathit{Solar.rad} + 0.35\mathit{Wind} + 0.21$	0.92
Bush honeysuckle	$0.78\mathit{Air.temp} -1.29\mathit{Solar.rad} + 0.19\mathit{Precip} - 0.37\mathit{Wind} + 4.12$	0.90
Armenian blackberry	$0.74\mathit{Air.temp} - 0.40\mathit{Solar.rad} + 0.21\mathit{Precip} + 3.48$	0.86
Wine raspberry	$0.72\mathit{Air.temp} - 0.77\mathit{Solar.rad} + 0.161\mathit{Precip} - 0.55\mathit{Wind} + 5.46$	0.87
Jetbead	$0.76\mathit{Soil.temp} - 0.40\mathit{Solar.rad} + 0.07\mathit{Precip} + 1.33$	0.96
Oriental bittersweet	$0.77\mathit{Soil.temp} - 0.29\mathit{Solar.rad} + 0.17\mathit{Wind} + 0.68$	0.92
Japanese honeysuckle	$0.87\mathit{Soil.temp} + 1.03\mathit{Solar.rad} + 0.82\mathit{Wind} - 1.10$	0.70
Crownvetch	$0.85\mathit{Soil.temp} + 0.82\mathit{Solar.rad} + 0.56\mathit{Wind} - 0.25$	0.85
Johnson grass	$0.94\mathit{Soil.temp} + 0.52\mathit{Wind} - 2.79$	0.82
Japanese stiltgrass	$0.81\mathit{Soil.temp} + 0.29\mathit{Wind} - 0.49$	0.91
Mixed exotics	$0.77\mathit{Soil.temp} - 0.43\mathit{Solar.rad} + 0.68$	0.95

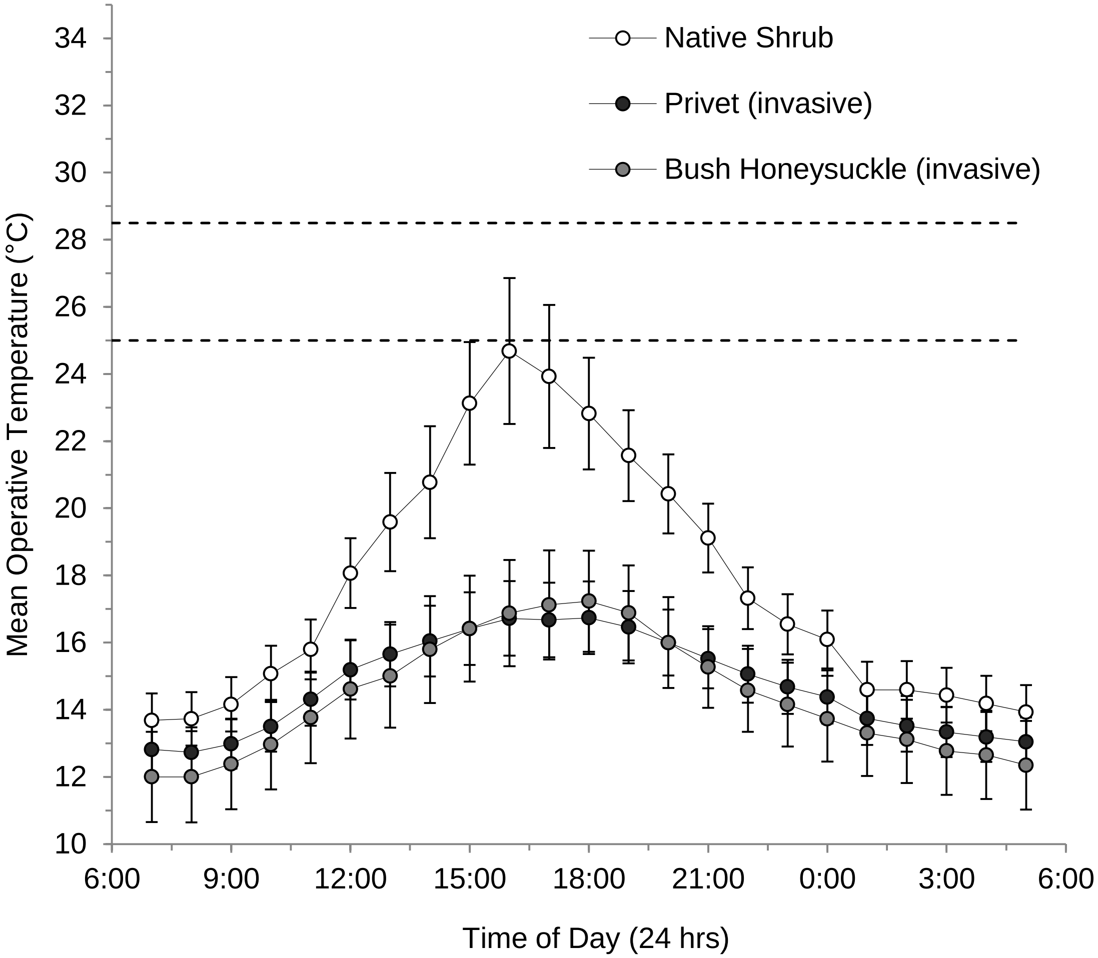

Figure A.1. Mean (±SE) hourly T_e at Northern Copperhead hibernacula dominated by native shrubs, privet, and bush honeysuckle during the month of May.

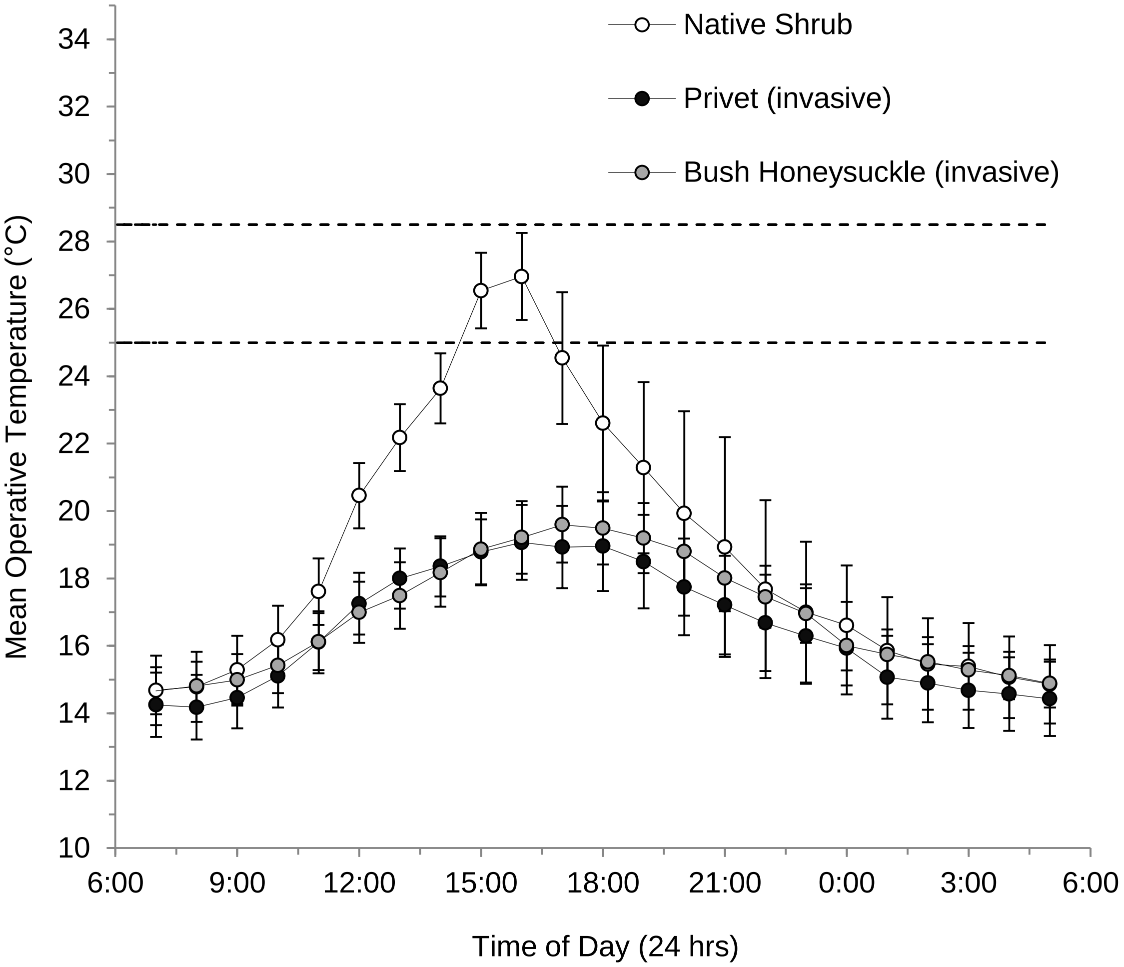

Figure A.2. Mean (±SE) hourly T_e at Northern Copperhead hibernacula dominated by native shrubs, privet, and bush honeysuckle during the final two weeks of May.

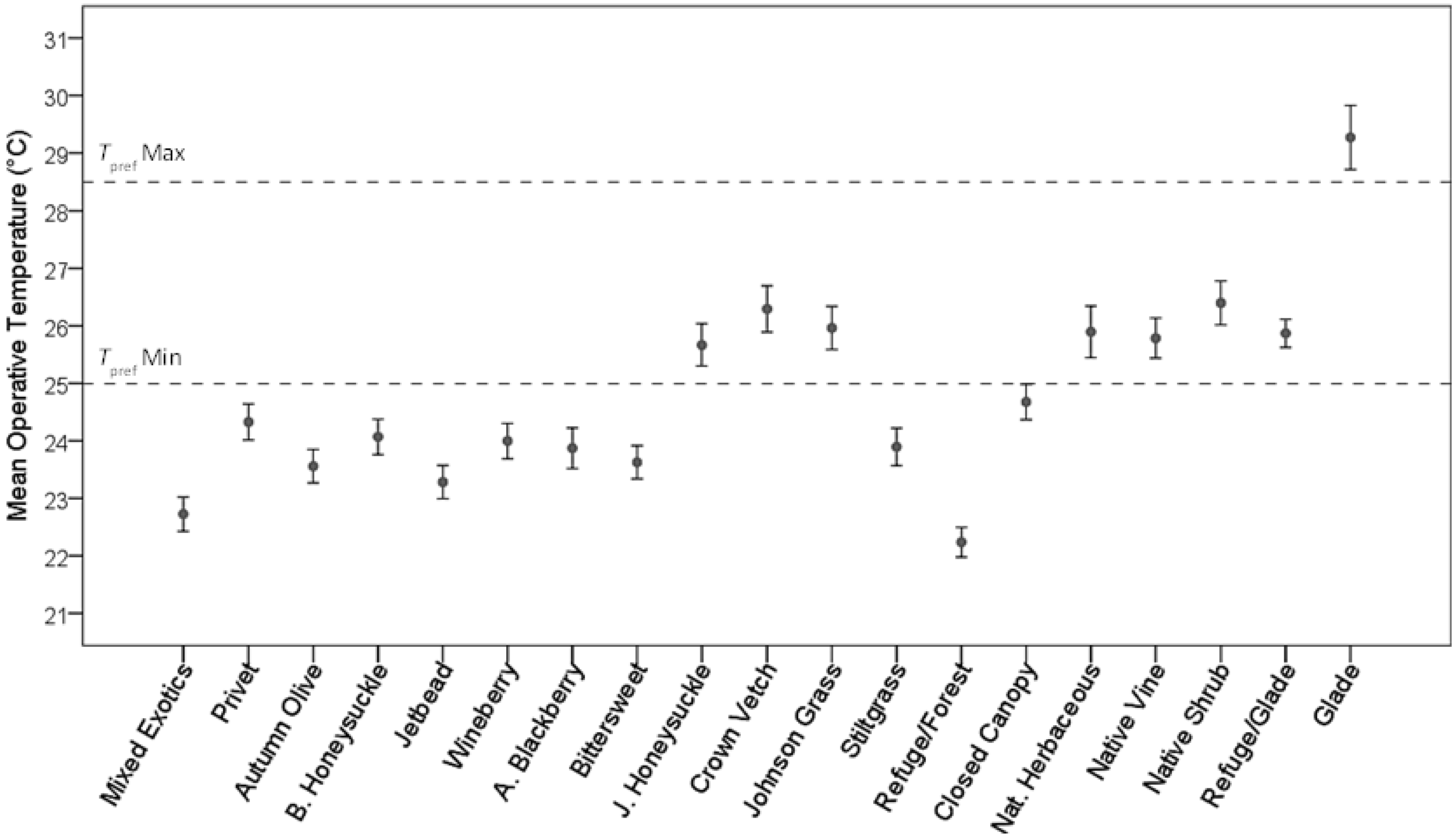

Figure A.3. 95% Bonferroni confidence intervals for mean T_e in native and exotic dominated habitats during the summer activity season after incorporating a 3 °C increase in air temperature based on projected climate change. Horizontal dashed lines represent the upper and lower extremes of the preferred body temperature range of Northern Copperheads.

Table A.5. Records and sources of fatal and nonfatal injury in telemetered Northern Copperheads during the course of the study (June 2008 – October 2011). An asterisk indicates that particular snake is listed more than once due to multiple injuries.

Snake ID	Date	Sex	Habitat	Source	Outcome
150.650*	Jul-08	F	Managed Gap	Brush pile manipulation	Nonfatal
150.590	Jul-09	F	Managed Gap	Woody vegetation control	Fatal
150.779*	Jul-09	M	Managed Gap	Herbaceous control	Nonfatal
150.510	Aug-09	F	Natural Gap	Predation	Fatal
150.550	May-10	F	Forest	Intentional Killing	Fatal
150.110*	Jun-10	M	Managed Gap	Woody vegetation control	Nonfatal
150.286	Jun-10	M	Managed Gap	Woody/herbaceous control	Nonfatal
150.271	Jul-10	F	Managed Gap	Herbaceous control	Nonfatal
150.779*	Aug-10	M	Managed Gap	Brush pile manipulation	Fatal
150.310	Sep-10	F	Natural Gap	Predation	Fatal
150.472	Apr-11	M	Forest	Predation	Fatal
150.581	Jun-11	F	Managed Gap	Woody/herbaceous control	Nonfatal
150.200	Jun-11	M	Managed Gap	Herbaceous control	Fatal
150.689	Jul-11	F	Managed Gap	Brush pile manipulation	Fatal
150.110*	Jul-11	M	Managed Gap	Herbaceous control	Fatal
150.250	Jul-11	M	Managed Gap	Herbaceous control	Fatal
150.610	Jul-11	M	Managed Gap	Herbaceous control	Fatal
150.650*	Aug-11	F	Managed Gap	Brush pile manipulation	Nonfatal
150.285	Aug-11	M	Managed Gap	Brush pile manipulation	Fatal