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A multi-scale evaluation of eastern hognose snake (Heterodon platirhinos) habitat selection at the northern extent of its range

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A MULTI-SCALE EVALUATION OF EASTERN HOGNOSE SNAKE (*Heterodon platirhinos*) HABITAT SELECTION AT THE NORTHERN EXTENT OF ITS RANGE

BY

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Date

DEDICATION

For my big sister Lucie.

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ABSTRACT

A MULTI-SCALE EVALUATION OF EASTERN HOGNOSE SNAKE (*Heterodon platirhinos*) HABITAT SELECTION AT THE NORTHERN EXTENT OF ITS RANGE

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Celine Goulet

University of New Hampshire, May, 2010

A complex interaction of biotic and abiotic variables structure landscapes into a hierarchal assemblage of habitats. Species respond to this environmental hierarchy by selecting habitat based upon a set of ecological variables occurring across a range of organizational levels. However, as the criteria for selection may be scale-dependent, it is vital to quantify the influence these variables have on species distribution at each spatial scale. Two years of telemetry data from 17 individuals were used to examine the multi-scale selection process in the northern population of *Heterodon platirhinos* on the New Boston Air Force Station in New Boston, New Hampshire. Thermal quality, habitat structure, prey availability, and predator avoidance were predicted to be the primary influential variables dictating the selective process in these ectothermic organisms, with the thermal environment being of particular importance. Statistical comparisons and modeling results revealed that snakes were selective at all three spatial scales, with thermal extremes and habitat cover being the dominant influential variables. At the landscape level, mixed forest maintaining environmental temperatures above thermal minima (7.0 ° C) were highly selected whereas at the home-range level, hemlock forests that did not exceed thermal maxima (40.5° C) were preferred. Overall optimal habitat was identified as having the following characteristics: 1) mixed and hemlock forests having continuous canopy and understory architecture interspersed with fine-scale openings; 2) close proximity to wetlands; 3) high density of leaf litter, debris, and rocks; and 4) homogeneous surface temperatures within critical thermal limits. Together, this structural configuration likely maximizes thermoregulatory precision while still conferring the secondary biological needs of predator avoidance and suitable prey availability.

CHAPTER I

INTRODUCTION

Introduction

Landscapes can be described as being mosaics of habitat patches. The ultimate configuration of these vegetative units is dictated by the interaction between biotic and abiotic variables, including climate, topography, soil, and population dynamics (Figure 1.1). Such processes occur at a hierarchy of spatial and temporal scales, integrating the constituent habitats and their associated environmental resources into a series of nested levels, where each level represents a shift in dominant structuring variables (Holling 1992; Johnson et al. 2004).

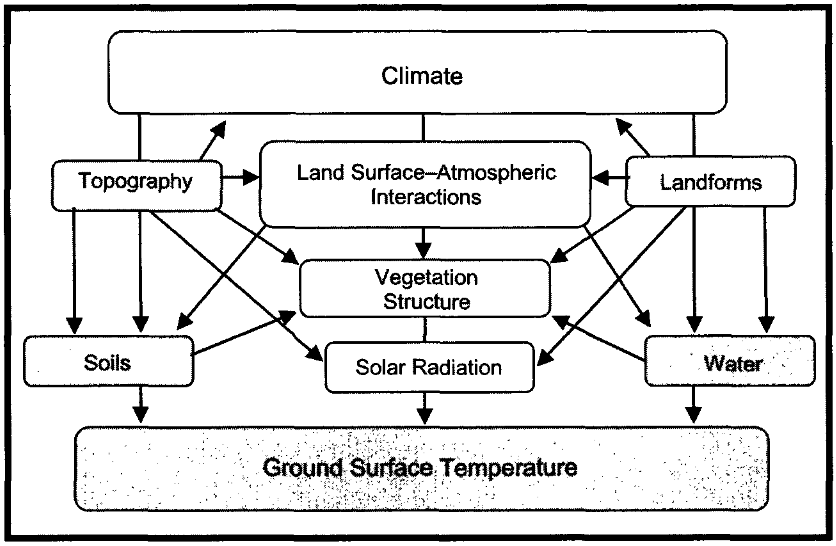

Figure 1.1. Environmental variables potentially influencing habitat selection at the regional, landscape, home range, and activity site scales.

Species respond to this hierarchal patch structure through habitat selection, a process by which an individual makes a choice to utilize a particular portion of the existing landscape. Selection is distinguished from utilization in that the level of a habitat's use is disproportionate to its availability (Johnson 1980). It has been suggested that proximate cues perceived at multiple spatial scales of resolution are used to discriminate among the available habitats, prompting a species to make a series of stepwise decisions; first by choosing a general habitat type in which to live, then making subsequent decisions about the use of different patches within that habitat type, and finally selecting an activity site from amongst those patches (Bergin 1992). The criteria for selection may be incongruent across spatial scales, where each level may have its own unique set of influential variables (Alldredge et al 1998; Morin et al 2005). There is, however, a direct relationship between the extent of distributional constraint imposed by a variable and the spatial scale at which species exhibit selective behavior to mitigate that variable. Those having the greatest potential to minimize individual fitness are conceivably avoided at the broadest spatial scales while less critical variables may instead influence habitat selection patterns at finer scales (Rettie and Messier 2000; McLoughlin et al. 2004). In this way, limiting factors dominate selective behavior at successively finer scales, whereby the extent of control is superseded by subsequently less prevalent limiting factors.

The degree to which a variable influences a species to select habitat is dependent upon its own intrinsic tolerance limits, as each species differs in its ecological requirements. This is especially evident in snakes, whose ectothermic strategy forges an inextricable link between body temperature and fitness. Accordingly, a snake's body temperature must be maintained within a relatively narrow range to optimize physiological performance. In achieving and subsequently maintaining such precise temperature preferences, snakes rely primarily upon their behavior as a thermostatic mechanism, where habitat selection, timing of activity, and posture act as filters transducing the surrounding thermal regime into a particular body temperature through radiative and conductive heat exchange. Very specific environmental conditions, particularly thermal conditions, are therefore imperative in fulfilling a snake's thermal requirements (Whitaker and Shine 2002, Herczeg et al 2006).

However, given that the thermal landscape is inherently variable, the extent to which behavioral thermoregulation is effective in protecting a snake from its critical limits is ultimately constrained by the range of thermal conditions present in a given environmental situation (Peterson et al. 1993). Physiological performance then hinges upon the snake's ability to correctly discern, and subsequently select, portions of the landscape that maximize its capacity to maintain thermal preferenda. Therefore, it was hypothesized that the habitat variable having the greatest impact on thermoregulatory efficacy at both the individual as well as population level, environmental thermal quality, would serve as the primary proximate factor influencing snake habitat selection across multiple scales. As these temperature gradients are under broad ecological control, determined by the interaction of a suite of abiotic variables including climate, landforms, vegetation structure, and soil type, it can be further predicted that variables exerting the greatest control over ground surface temperature at each spatial level would, in turn, have a secondary influence on habitat selection.

Selection of Geographic Range

The first scale of habitat selection is that of geographical range (Johnson 1980). A species' geographic range is the spatial extent over which all populations of that species occur. At this scale, geomorphic processes manipulate the land surface, creating a variable expanse of landforms and hydrologic features. Such formations, coupled with limited dispersal capabilities, act as physical barriers to snakes, impeding range extension. Physiography further limits overall species distribution as it interacts with prevailing weather systems to establish regional precipitation and solar radiation patterns. The resulting environmental gradients of temperature and moisture have direct consequences to long-term viability of snakes, and thusly, form boundary conditions that determine the spatial arrangement of species across the landscape (Swanson et al. 1988). As such, snake habitat selection within this geographic context is determined by the interaction between the broad-scale climatic factors and a species' physiology, where thermostatic variables exert the greatest overall selective pressure, thereby, initiating the habitat selection process (Reinert 1993).

Selection of Landscape Range

Landscape scale is the second order of habitat selection. At this hierarchal level, local physiography, by its elevation, aspect, and parent materials, modifies geographic-scaled inputs of environmental resources to produce a heterogeneous mosaic of habitat patches. Within each of these patches, variation in vegetation interacts with terrain attributes to influence heat exchange as well solar emissivity at the ground-atmosphere interface, generating a habitat unit characterized by its own array of climatic conditions. Distribution of snake populations throughout this dynamic landscape matrix is a direct response to the resultant size and isolation of these structurally, and thus, thermally explicit habitat patches. Accordingly, landscape scale selection in snakes is most likely prompted by the proximal availability of divergent patches, which, as an assemblage, provide a range of thermal opportunities critical to meeting the physiological requirements of the population as a unit.

Selection of Home Range

The third level of the hierarchal selection framework is the home range. The home range encompasses an area within which an individual of a population performs all of its biological functions during a typical activity cycle. Given the resources necessary for fulfilling these functions are rarely uniformly distributed across the landscape, the size and shape of a home range is, therefore, dictated by the spatial and temporal availability of such resources (Waldron et al. 2006).

For snakes, home range selection is primarily driven by seasonal physiological needs where reproductive condition, age class, and ecdysis all require specific resources, in particular, specific prey and thermal resources. As gape-limited predators, snakes must utilize habitats which provide sufficient prey densities of the appropriate size and type to meet energy requirements throughout the active season (Seigel and Collins 1993; Weatherhead et al. 2003). Nonetheless, because both foraging and digestive efficiency are related to body temperature, it has been suggested that thermoregulation takes precedence over all other requirements, including feeding (Wills and Beaupre 2000). As a result, microclimate heterogeneity, and to a lesser extent prey distribution, are variables that serve to influence home range selection among snake species, with this choice reflecting a conflict between food availability and thermal stress (Huey 1991).

Selection of Activity Site

The fourth scale of habitat selection is the selection of activity sites. The activity site constitutes the use of specific habitat components within the home range and is quantified by a suite of physical and biological variables that influence the allocation of time and energy expended by an individual (Morris 1987; Bergin 1992). Abiotic variables, in particular vegetation physiognomy, dictate the fine-scaled structural configurations associated with each site. Heterogeneity in vertical vegetation structuring as well as horizontal surface composition produces a diverse pattern of light, temperature, and moisture conditions (Mackey et al. 2001). Distribution of these water and solar resources are further influenced by the soil type occurring within the site, where compactness as well as thermal properties varies with surficial matrix structure (Johansson et al. 2006). Because the immediate physiologic processes of digestion, locomotion, and reproduction are all related to a snake's body temperature, individuals respond to these static physical structures as they serve as indicators of microclimatic conditions and refugia availability. Selection by snakes at this fine scale is, therefore, driven primarily by the superimposition of microclimatic features onto the geometric configuration of the environment, where these visual cues are used to remotely evaluate sites in terms of thermal quality (Waldron 2006).

Activity-site selection may be further influenced by the snake's morphological attributes as well, in particular dorsal color (Bittner et al. 2002). Variation in body coloration is common among squamates whereby individuals of polymorphic populations typically occur as either wild-type or melanic morphs. Such intra-specific variability in body coloration, while probably established through genetic drift, is maintained through strong natural selective processes with thermoregulatory and cryptic adaptations being the primary agents (Rosenblum et al. 2004). In cool climates where snakes are exposed to severe environmental temperatures and restricted by short activity seasons, melanistic individuals are presumably selected for over wild types as melanism affords the advantage of increased heat absorption efficiency. Being of the melanic variant may, thusly, serve to broaden an individual's range of thermal preferenda, minimizing elevational and longitudinal microhabitat constraints, and thereby, enabling cooler climatic conditions to be exploited both temporally as well as spatially (Vences et al. 2002). Conversely, expanded suitability of the thermal environment may be countered by the reduction in crypsis incurred by the melanic trait. With an increase in exposure to visual predators due to lack of substrate matching, melanistic individuals would potentially be excluded, either behaviorally or through predation, from activity sites having environmental features which inhibit crypsis, as predatory pressure would be greatest in such habitats (Bittner et al. 2002). As a result, activity site selection would likely be a response to thermoregulatory efficiency associated with morphological condition coupled with fine scale habitat attributes.

Study Species

The eastern hognose snake (*Heterodon platirhinos*) is a relatively poorly studied species that is considered to be of regional concern in the northeastern United States (Therres 1999) and is listed as endangered in New Hampshire (New Hampshire Endangered Species Conservation Act RSA 212-A, New Hampshire Fish and Game Threatened and Endangered Wildlife List Administrative Rule FIS 1000). *H. platirhinos* has a widespread but scattered distribution throughout much of southern Ontario and eastern United States where it is associated with open woodlands, grasslands, and fields occurring on sandy, well-drained soils (Michener and Lazell 1989). Use of such xeric habitats may be an artifact of this species' thermal specialization, where it requires thermally homogenous sites in order to maintain its relatively high preferred body temperature (Cunnington 2006; Plummer and Mills 2000).

New Hampshire represents the northern range limit of *H. platirhinos*, where isolated disjunct populations occurring in low densities are restricted to the Merrimack River corridor (Michner and Lazell 1989). Unlike the more central portions of its distribution, specific habitat associations have not been determined for the New Hampshire population of *H. platirhinos*. Making broad assumptions by pooling divergent populations, such as those in New Hampshire, has the potential to mask meaningful biological information concerning local habitat affinities (Reinhart 1984). Therefore, identifying the distinctive spatial and behavioral ecological attributes specific to each population, especially peripheral populations, would contribute substantially to our understanding of the variables that influence habitat selection and resultant distribution of this species (Larsen and Gregory 1989).

Objectives

Given its protected status, unquantified habitat associations, and narrow thermal preferenda, this northern population of *H. platirhinos* provided an exemplary opportunity to investigate the topic of multi-scale habitat selection in peripheral snake populations. A series of statistical and modeling approaches were utilized to test the hypothesis that the thermal environment, and the variables regulating that environment, were the dominant variables governing habitat selection across the hierarchal spectrum, particularly at finer scales of resolution. Hierarchal analysis was first used to examine the scalar selection pattern of *H. platirhinos* within its northern distribution. This approach served to: 1) detect the occurrence of habitat selection at the landscape, home range, and activity site spatial scales; and 2) identify the variable(s) having the greatest selective influence at each of these spatial scales. Upon discerning the set of critical variables, they were then utilized in developing a predictive model identifying optimal habitat in a landscape context. To further test the preeminent role thermostatic variables played in the selective process, environmental thermal quality was assessed and thermoregulatory efficiency measured.

CHAPTER II

METHODS

Study Area

The study was conducted on the 1144 ha New Boston Air Station (NBAS) located in Hillsborough County in south-central New Hampshire (Figure 2.1). Dominant land-cover types include mixed (40.2 %) and deciduous forests (29.3 %), with forest stands comprised of 25-55% coniferous basal area per acre being considered mixed and those comprised of less than 25% coniferous basal area per acre being classified as deciduous. Eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubrum*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and red maple (*Acer rubrum*) are the most abundant species (LaGory et al. 2009). Forest management includes both selective and small clearcuts (Argonne National Laboratory 1997). Topography is hilly with an elevation range of 104 m msl to 389 m msl. Canton series fine sandy loam is the dominant soil. The regional climate is characterized as humid continental, with an average annual temperature of 8.0 C and monthly averages range from -5.2 C in January to 21.0 C in July (Argonne National Laboratory 1997).

Capture, Monitoring, and Home Range Estimation

Surveys to capture snakes began in mid-April and continued through September. Captured individuals were measured (TBL), weighed, and assigned an age class based on weight: (*hatchlings* < 10 g; *juveniles* 10-100 g; *adults* > 100 g). For all adult, non-gravid, snakes (> 200 g), temperature sensitive transmitters (Advanced Telemetry Systems, Model F1820t) were surgically implanted by a cooperating veterinarian following the procedures described by Reinert and Cundall (1982). Radio-tagged snakes were located at approximately 2-day intervals utilizing a portable receiver (Communications Specialists, Model R-1000) equipped with a three-element Yagi antenna (Communications Specialists, Model RA-150). Locations were determined by homing, a non-triangulation technique where the transmitted signal is followed until the instrumented animal is observed (White and Garrott 1990). This method was used to facilitate surface temperature and solar radiation measurements of occupied sites. Behavior (*active* = on ground surface or *inactive* = in retreat or no visual) and locational data were also collected at each relocation.

The fixed kernel density estimator with least squares cross validation was employed using Hawth's Tools Extension in ArcGis 9.0 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to delineate snake home ranges. Fifty percent, 75%, and 95% isopleths were created for each individual. Home range delineation was limited to snakes tracked during the 2008 season having $\geq$ 15 marked locations and tracked for > 50 d. Selection analyses were restricted to these individuals for which home ranges were calculated.

Multi-Scale Habitat Characterization and Selection

Landscape Scale

Characterization The landscape scale was characterized by both land cover and thermal environment. The available landscape was estimated by overlaying the union of all 95% kernel home ranges onto the study area. The digital land-cover data layer (GRANIT 2002) was reclassified into 11 categories: developed (DV), field (FI), beech/

oak/ hardwoods (BOH), birch/ aspen (BA), white/ red pine (WRP), hemlock (HM), mixed forest (MF), disturbed (DI), and cleared (CL) with wetlands being excluded from the selection analyses as this species is strictly terrestrial (Figure 2.2). Habitat metrics including total area, habitat types present, number of habitat patches, area of each habitat type, and percent cover were calculated using the Patch Analysis extension of ArcGIS (Environmental Systems Research Institute, Inc., Redlands, California, USA).

To quantify the available range of thermal options, ground surface temperature (GST) was collected using Thermochron iButton temperature data loggers (Embedded Data Systems DS1921G, accuracy ±1 C). In late May, 116 data loggers were systematically placed 300 m apart in a grid formation throughout the entire study area, excluding roads, water bodies, and station operation areas. Each data logger was inserted into a plastic fob and secured to the ground with a stake. Temperature was collected every two hours for the duration of the study. At the onset of hibernation, data loggers were de-activated and data retrieved using the OneWireViewer program (Dallas Semiconductor Maxim Version 1.3). Georeferenced data logger data were imported into a GIS and interpolated to calculate landscape-scale temperatures. Minimum, mean, and maximum temperature range data layers were generated for the entire activity period (*overall* = May through October) as well as by season (*spring* = May through June, *summer* = July through August, and *fall* = September through October). Interpolated thermal data for each layer was reclassified into 9 temperature classes. Overall minimum and maximum range data layers were then utilized in snake habitat model development.

Habitat Selection Habitat selection at the landscape scale was quantified using compositional analysis (CA) (Aebischer et al 1993). At this scale, availability for all animals was delimited by the landscape range, whereas use was delimited by the union of all home ranges. Proportional use and proportional availability of each habitat was calculated for each snake. Available habitat types that were not used were replaced with small, non-zero value (0.003) as suggested by Bingham and Brennan (2004). In doing so, undefined log-ratios were avoided and Type I errors minimized while still maintaining the integrity of undetected use. Log-ratio transformation was conducted separately for the matrices of used and available data to remove linear dependency (Pendleton et al. 1998). Use and availability composites were obtained using the software package Biotas (Ecological Software solutions 1998). Testing of nonrandom habitat use was performed in JMP 7.0 (SAS Institute 2007) using the test statistic Wilk's lambda (Λ). With the occurrence of habitat selection, differences between log-ratios were averaged across animals to obtain a mean for each habitat type and then ranking matrices were created to assess relative preferences (Johnson 1980). Habitat types with use-availability ratios significantly greater than 0 were considered preferred whereas those significantly less than 0 were considered avoided. Univariate paired *t*-tests were then used to identify which habitat types were selected for significantly different than others (Pendleton et al. 1998). Thermal data collected in selected habitat types were analyzed to assess thermal preferences.

Home Range Scale

Characterization Home range selection was evaluated in terms of land cover and primary prey availability. Habitat metrics including total area, habitat types present, number of habitat patches, area of each habitat type, and percent cover within individual home ranges (95% isopleth) were calculated using Patch Analysis for ArcView 9.0. A habitat suitability model was developed to determine prey (*Bufo americanus*) distribution within individual home ranges (Appendix B). The resultant model predictions were intended to be utilized in developing the snake habitat model. However, as the *B. americanus* habitat suitability model performed poorly, the selective influence of prey availability could not be assessed nor could the generated data layers be incorporated into the *H. platirhinos* habitat model.

Habitat Selection Habitat selection at the home range scale was quantified using the same methodology as that of landscape selection. However, availability at this scale was defined as the proportion of each habitat type within an individual's 95% fixed kernel home range and use was considered as the percentage of radio locations within each habitat type (McLoughlin et al 2004).

Activity-Site Scale

Characterization The activity-site was characterized in terms of habitat and predation. Habitat was described using 2 climatic and 17 structural features (Table 2.1). Sampling was conducted in 5-m radius plots centered on the locations occupied by the snake within 2 weeks of the individual vacating the site. For each location, an associated random site within 0-50 m (95% confidence interval of the mean daily movement) was identified. The same suite of habitat and climatic variables was recorded at the random sites and marked with a GPS. These sites were sampled within 15 min of associated snake location sampling. Differential predation was examined in the field using plasticine models to assess the effects predation vulnerability has on activity-site selection between morphs (refer to Appendix C for detailed summary).

Table 2.1. Activity site habitat characterization variables. Climatic and structural variables were measured at each snake location and random location.

Variable	Description	Method of Measurement
ELEVLAND	Elevation at 5 m resolution	Calculated using Arc View Spatial Analyst
ASPECT	Aspect	Calculated using Arc View Spatial Analyst
CANOPY	Percent canopy closure	Visually estimated closure utilizing paper cylinder
OVERDIST	Distance to nearest overstory[1] tree	Measured from center of plot to closest point of tree up to 20 m
OVERDBH	DBH of nearest overstory tree	Measured using DBH tape
UNDERDIST	Distance to nearest understory[2] tree	Measure from center of plot to closest point of tree up to 20 m
UNDERDBH	Diameter at breast height of nearest understory	Measured using DBH tape
SHRUBIST	Distance to nearest shrub	Measured from center of plot to closest point of shrub up to 20 m
RETREAT	Distance to nearest retreat	Measured from center of plot to closest point of retreat site up to 20 m
LEAFDEPTH	Leaf litter depth	Measured depth at center of plot
LEAFDENS	Percent leaf litter coverage	Visually estimated
DEBRIS	Percent downed woody debris coverage	Visually estimated
HERBDENS	Percent herbaceous cover	Visually estimated
SOILDENS	Percent bare soil coverage	Visually estimated
STUMPDENS	Percent stumps coverage	Visually estimated
SURFTEMP	Surface temperature	Measured snake locations with digital hygrometer
SLOPE	Degree of slope	Visual estimated
LAI	Leaf Area Index	Hemispherical photos taken at center of plot and analyzed using GLA software
SOLRAD	Solar radiation	Hemispherical photos taken at center of plot and analyzed using GLA software

[1] Overstory is defined as vegetation with a DBH of $\geq$ 7.5 cm
[2] Understroy is defined as vegetation > 2 m in height with a DBH < 7.5 cm

Habitat Selection Prior to analysis, Pearson correlation coefficients were examined to minimize multicolinearity among the 21 variables. One variable from pairs of highly correlated ($r > 0.7$) variables were removed from the analyses. Multivariate analysis of variance (MANOVA) was used to test if used and random sites differed. Stepwise Discriminant Analysis (DA) was used to: 1) examine the difference among group centroids between used and random locations; and 2) identify specific variables which contribute most strongly to group separation (Blouin-Demers and Weatherhead 2001). Model inclusion was based on univariate ANOVAs for each of the variables, with order of entry corresponding to the relative discriminating ability of individual covariates. Significance of the final model was determined by the Wilk's Lambda (Λ) test statistic. Analyses were repeated using all combinations of removed variables to compare discriminate function significance and model performance. Linear correlations between variables and resultant discriminant function were examined for biological meaning. Stepwise logistic regression was then used to model activity-site selection. A significance level of 0.05 was used for entry and retention to build the model. Ultimate inclusion into the final model was based on the likelihood function. Model performance was measured by the lack of fit test.

Seasonal selection was visually assessed by overlaying locational and land cover data layers. Utilized habitat types were categorized by season (*breeding/ nesting* = emergence to mid-July, *non-breeding* = mid-July to mid-September, and *hibernation* = mid-September to emergence) and compared to detect seasonality in habitat preferences. Statistical analysis of seasonal habitat selection was not performed as sample size was insufficient.

Thermoregulation Thermoregulation was evaluated to discern if thermal quality was the primary determinant of activity-site selection for *H. platirhinos*. High quality habitat was characterized as thermally homogenous sites promoting the maintenance of preferred body temperatures with minimal thermoregulatory cost. By contrast, low quality habitat was characterized as sites which did not provide such opportunities experiencing extreme thermal conditions, thereby, requiring greater energy to be invested in thermoregulation. Following the approach suggested by Row and Blouin-Demers (2006), thermoregulation was evaluated using the following data: body temperatures (T_b) of field-active snakes, operative environmental temperatures (T_e) representing the T_b of non-thermoregulating snakes, and the species-specific range of preferred body temperatures (T_{set}) (Hertz et al. 1993). Individual snake T_b measurements were determined by temperature-sensitive radio transmitters implanted into the study snakes (refer to *Capture and Monitoring*). Available T_e distributions were constructed from data logger surface temperature data (refer to *Landscape Characterization*), and T_{set} was based on laboratory experiments conducted by Platte (1969). These data were then used to estimate three thermoregulation indices, accuracy of thermoregulation (d_b) calculated as the mean of the deviations of T_b from T_{set}, thermal quality of habitat (d_e) calculated as the mean deviations of T_e from T_{set}, and effectiveness of thermoregulation (E) calculated as the difference between d_e and d_b, which together serve to quantify the magnitude of thermoregulatory behavior as well as the availability and exploitation of optimal thermal habitat. High selective influence of thermal quality was inferred by positive values of E ($d_b < d_e$), such that T_b was closer to T_{set} than one would expect from non-thermoregulating snakes (Hertz et al. 1993).

Body and environmental data were subjected to tests for normality and heterogeneity of variances prior to analysis. Body temperature data of 6 snakes were pooled. Operative environmental temperature measurements from data were grouped into one of three habitat categories: developed, early successional, or forest. An hourly mean T_e and d_e was calculated for each habitat type. Mean T_e and d_e values were extracted for each hour during which a snake was located. Individual measurements and indices of each location were averaged to produce mean T_b, T_e, d_b, d_e, and E values. Intra-habitat variances were examined as a measure of thermal homogeneity. ANOVA was used to test whether T_b and E varied by habitat type. All statistical analyses were conducted using JMP 7.0.

Habitat Model Development

Model Framework

A habitat model was developed in ArcView 9.0 to predict ideal *H. platirhinos* habitat based on the Mahalanobis (D^2) distance statistic. The distance measurement represents the difference between the mean vector of occupied sites and unoccupied sites scaled by the variance and covariance of predictor variates (Johnson et al. 2005). The resultant Mahalanobis statistic provides a dimensionless index of similarity to landscape conditions associated with ideal habitat in multivariate space (Knick and Rotenberry 1998). As an inverse relationship exists between the D^2 value and the magnitude of similarity, greater similarity to ideal habitat is indicated by small values whereas larger values are interpreted as greater dissimilarity, hence lower quality habitat. This modeling technique has proven advantageous as it ignores the assumptions of multicolinearity as well as normality (Knick and Rotenberry 1998; Browning et al. 2005). What's more, only presence data are required, thereby, avoiding the problems associated with classifying available habitats as unused.

Explanatory variables influential to snake habitat selection were chosen *a priori*. Initially, these factors were to include surface temperature, elevation, slope, aspect, soil type, land cover, and prey density. However, prey density was omitted from the analysis as the suitability model demonstrated low predictive ability. Thus, the snake habitat model was based on the remaining 7 variables. Surface temperature data layers were generated using thermal data collected from data loggers. Thermal layer coverage was restricted to the study site as environmental measurements were not collected beyond NBAS boundaries. Overall minimum and maximum temperature ranges for the entire activity period were calculated for each georeferenced data logger location. Data were interpolated using the kriging method and then reclassified to generate minimum and a maximum mean temperature data layers. Elevation was derived from digital elevation models (GRANIT 2002). Spatial Analyst (Environmental Systems Research Institute, Inc., Redlands, California, USA) was used to generate slope and aspect. Slope was represented in degrees and aspect was represented degrees from north. To meet analysis requirements, soil type data was converted to a quantitative format based on the physical property bulk density using the Soil Survey Geographic Database (SSURGO). This property was selected as its value is influenced by texture, organic matter content, and soil structure, attributes affecting *H. platirhinos* burrowing behavior. Categorical land cover data was converted to a numeric diversity grid using the Neighborhood Statistics function in Spatial Analyst. The variety option of this function was selected to determine the number of unique vegetation types within a 3 x 3 rectangular neighborhood. The

Mahalanobis Distances extension (Jenness 2003) was used in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to generate a D^2 surface 25 x 25 m resolution grid for all pixels in the study area based on the 7 explanatory variable data layers. The surface grid was recoded into a *p*-value grid on a 0 to 1 scale, where the *p*-values represented the probability of observing a D^2 value as large or larger than the actual D^2 (Thatcher 2006). *P*-values closer to 1 indicated a greater similarity to ideal landscape conditions, and thus more favorable habitat, as defined by snake locations.

Model Evaluation

A cumulative frequency distribution graph was constructed to test model predictions. The graph was based on two sets of locations and their associated D^2 values: (1) 150 snake locations and (2) a set of random locations (null model, $n = 150$) (Thompson et al. 2006). Snake locations were derived from telemetry data collected in 2008 while random locations were generated using the Hawth's Tools extension in ArcView 9.0. Both sets of data points were plotted on the D^2 surface grid to determine distance values. Percent cumulative frequencies of locations were graphed against the D^2 values. A threshold value was identified by determining the D^2 score which produced the greatest separation between snake locations and the null model frequency distributions. The selected threshold was then used to evaluate model accuracy as defined by the proportion of correct classification of snake locations. Both 2008 and 2007 telemetry data were overlaid onto the D^2 surface grid and the correct classification rate was calculated. Telemetry data were restricted to snake locations occurring on the NBAS study area as this was the spatial extent of the model data layers. Dependent on model performance, suitability of each pixel was assigned based on its associated D^2 value. Pixels with D^2 values below this threshold were indicative of more favorable habitat whereas pixels with larger values were considered less favorable.

Principal components analysis (PCA) was then performed to identify the partitioning of variation among habitat variables at classified sites. Eigenvalues and eigenvectors were generated using JMP 7.0. Relationships between variables and principle components were discerned by examining the loading matrix. Components with eigenvalues > 1 represented combinations of input variables describing the greatest amount of dissimilarity among snake locations where heavily weighted variables contributed most to the overall variance (Watrous et al. 2006). In contrast, variables having large eigenvectors corresponding to the lowest non-zero eigenvalues (< 1) were those that were uniform across utilized locations and, therefore, most informative in delineating favorable habitat (Rotenberry et al. 2002).

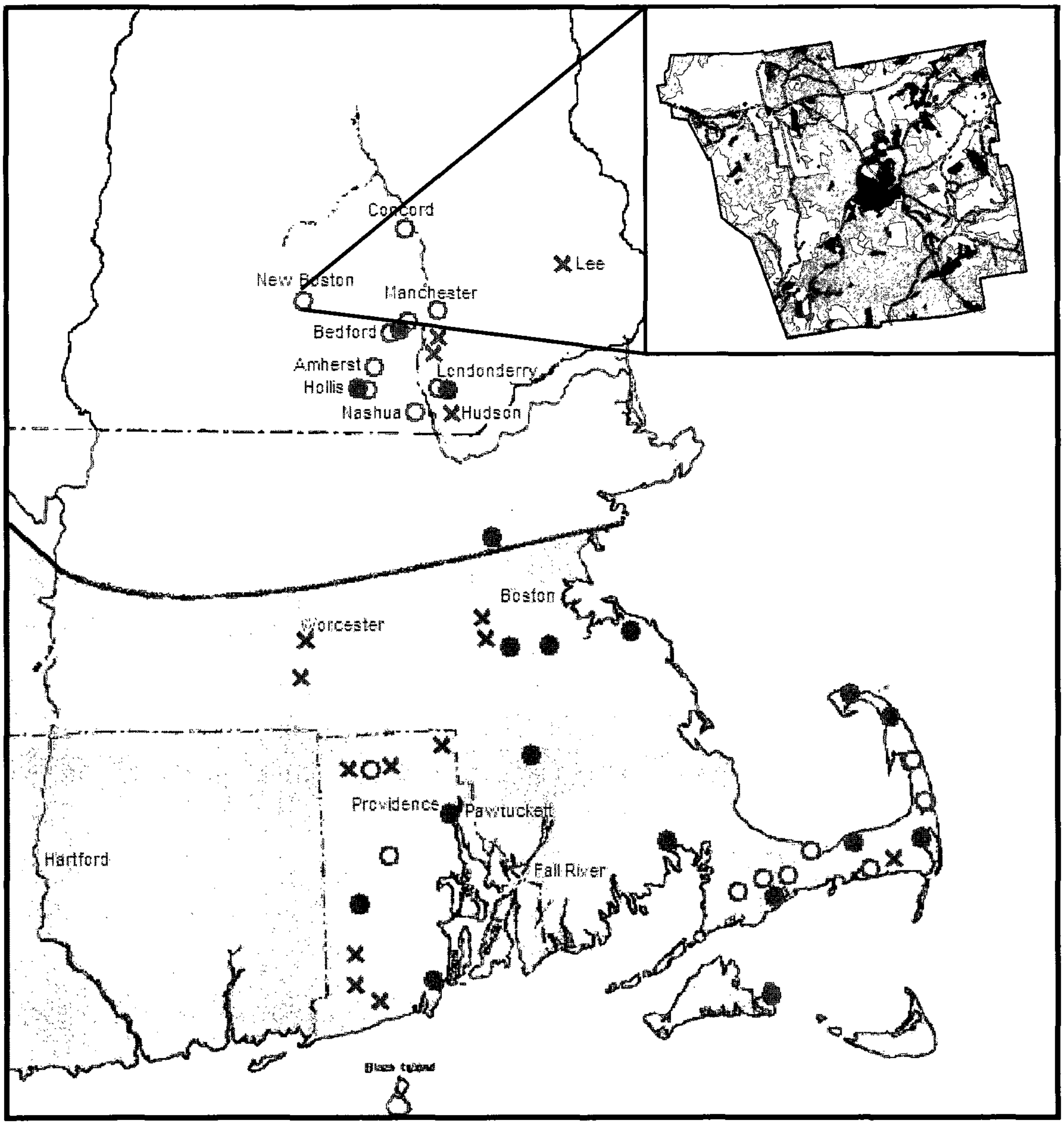

Figure 2.1. Regional distribution of *H. platirhinos*. Regional map and locations is a modification of that created by Lazelle and Michner (1989). Additional locations were provided from the New Hampshire Fish and Game Department. Open circles denote verified occurrence data, closed circles denote unverified occurrence data, x markings denote museum specimens, and gray area indicates continuous geographic range (Conant 1975).

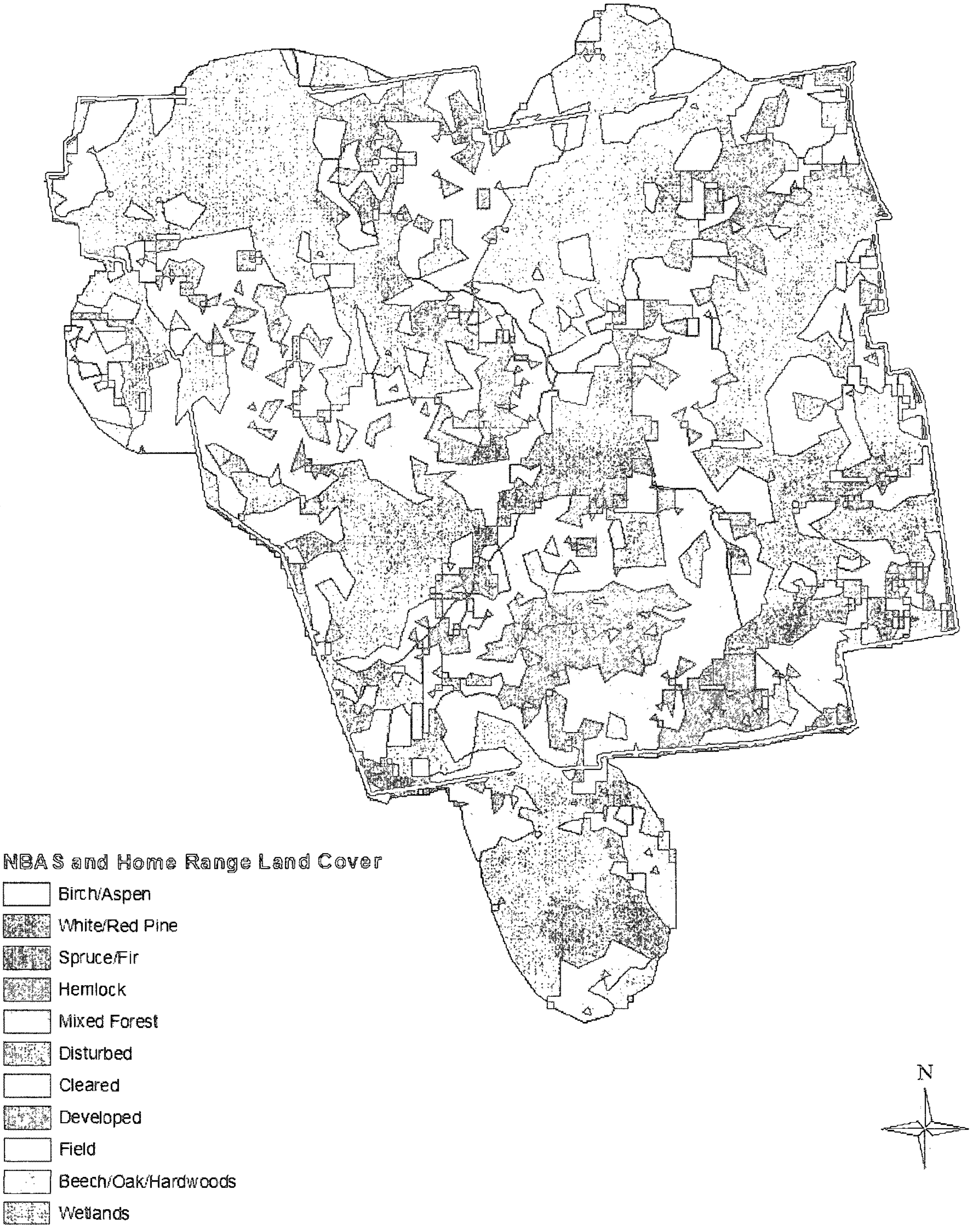

Figure 2.2. Reclassified land cover types occurring at the landscape range encompassing the union of the NBAS and home ranges of all 2008 *H. platirhinos* individuals.

CHAPTER III

RESULTS

Capture, Monitoring, and Home Range Estimation

Snakes were monitored from May 2007 through October 2008 (Table 3.1). A total of 25 snakes (2007 $n = 13$, 2008 $n = 12$) snakes were captured over the course of the study, 17 of which were implanted with radio transmitters and monitored. In 2007, tracking durations of the 9 transmitted snakes extended over periods of 9 to 231 days, with relocations per individual ranging from 4 to 34 locations ($\mu = 15.1$). In 2008, 7 transmitted snakes were tracked for a period of 12 to 141 days with relocations per individual ranging from 3 to 45 locations ($\mu = 22.6$). Telemetry data collected in 2008 were used in habitat selection analyses and model development whereas 2007 data served to evaluate subsequent model predictions.

Five snakes were used in the home range analysis (Figures A.1 – A.5). Total marked locations per individual ranged from 15 – 45 ($\mu = 31.40$). Individual 50%, 75%, and 95% kernel home range sizes ranged from 30.66 – 155.87 ha ($\mu = 62.25 \pm 51.17$ ha), 84.40 – 306.68 ha ($\mu = 138.05 \pm 94.52$ ha), and 179.19 – 588.33 ha ($\mu = 281.80 \pm 172.26$ ha), respectively. Overall home range area encompassed 834 ha with overlap ccurring between 4 of the 5 snakes.

Multi-Scale Habitat Characterization and Selection

Landscape Scale

Thermal Environment Analysis of the thermal environment was restricted to a 1095.5 ha area encompassing the data loggers. Of the 116 data loggers deployed, 69 successfully collected temperature while the remaining 47 data loggers did not take any measurements due to technical issues. Thermal data collection occurred from 30 May to 26 October resulting in a total of 118,505 temperature readings. Raw surface temperatures ranged from -20.5 to 59.5° C. Overall landscape-scale temperatures derived from the GIS interpolation method ranged from -2.6 to 29.6° C with -0.1 – 0.4° C (36.1 % total area), 7.1-8.9° C (22.4 % total area), and 15.2-16.9° C (22.4 % total area) temperature classes being most extensive for each of the minimum, mean, and maximum thermal coverages, respectively. Interpolated seasonal temperatures ranged from 2.2 to 18.3° C, 2.2 to 19.3° C, and 1.2 to 13.2° C for spring, summer, and fall, respectively. Among these ranges, the 5.9-7.6° C, 6.1-7.9° C, and 5.3-6.5° C classes had the highest spatial frequency (51.4 %, 41.5 %, and 51.9 % total area) during each respective season.

Habitat Selection Overall habitat use at the landscape scale was non-random with respect to availability (Wilk's $\Lambda = 3.21^{-17}$, $p = .001$). Compositional analysis indicated that developed, mixed forest, white/red pine, hemlock, and field were preferred whereas avoided habitats included birch/aspen, spruce/fir, cleared, disturbed, and beech/oak/hardwoods (Table A.1). The ranking matrix ordered the following sequence: developed > mixed forest > white and red pine > hemlock > field > birch/aspen > spruce/fir > cleared > disturbed > beech/oak/hardwoods. Developed habitat was selected significantly more than spruce/fir ($t = -2.20$, $p = 0.03$), cleared ($t = 2.37$, $p = 0.02$), disturbed ($t = -2.54$, $p = 0.02$), and beech/oak/hardwoods ($t = 3.05$, $p = 0.00$) (Figure 3.1). And mixed forest was selected for significantly more than disturbed ($t = 2.20$, $p = 0.03$) and beech/oak/hardwoods ($t = 2.71$, $p = 0.01$). Associated environmental temperatures of the highly selected mixed forests avoided extreme minimum temperatures, ranging from

-5.5 to 54° C whereas the highly avoided beech/oak/hardwood habitat was highly variable with temperatures ranging from -20.5 to 47.5° C.

Home Range Scale

Prey Availability The *B. americanus* model indicated that high prey densities were available within all five snake home ranges. However, based on model validation results, no significant correlation was detected between prey availability and *H. platirhinos* home range selection.

Habitat Selection Habitat use at the home range scale was significantly non-random with respect to availability (Wilk's $\Lambda = 0.23, p = .001$). Compositional analysis indicated that hemlock, white/red pine, mixed forest, and beech/oak/hardwoods were preferred whereas avoided habitats included disturbed, cleared, spruce/fir, developed, field, and birch aspen (Table A.2). The ranking matrix ordered the following sequence: hemlock > white/red pine > mixed forest > beech/oak/hardwood > cleared > disturbed > spruce/fir > developed > field >birch/aspen. Hemlock habitat was selected significantly more than cleared ($t = 3.00, p = 0.00$), disturbed ($t = 3.00, p = 0.00$), spruce/fir ($t = -3.07, p = 0.00$), developed ($t = 3.14, p = 0.00$), field ($t = 3.14, p = 0.00$), and birch/aspen ($t = 3.44, p = 0.00$) (Figure 3.2). Associated environmental temperatures of the highly selected hemlock habitat category did not achieve extreme maximum temperatures, ranging from -1.3 to 25.5° C ($\mu = 7.5$° C) while the highly avoided developed and field habitats (birch/aspen did not occur within home ranges) were highly variable with temperatures ranging from 1.5 to 59.5° C ($\mu = 18.3$° C).

Activity-Site Scale

Predation Avian predation was visibly discerned by the type of markings present on the attacked model. However, variation in predation frequency between color morphs was not detected due to insufficient data. Accordingly, this variable was not included in further selection analyses.

Habitat Selection The variables ASPECT, CANOPY%, LAI, RETREATDIST, and UNDERDIST were highly correlated with other variables (ELEV $r = 0.97$, SOLRAD $r = 0.97$, LAI $r = 0.97$, and OVERDIST $r = 0.90$) and thus were removed from the analyses. The overall MANOVA of the remaining 17 variables indicated that used and random sites differed significantly ($F = 3.62, p < 0.0001$). The single discriminant function derived from the stepwise DA was significant (eigenvalue = 0.17, $\Lambda = 0.85$, p-value < .0001) suggesting that that *H. platirhinos* used habitat nonrandomly at the activity site scale. The final model, comprised of SOLRAD, SHRUBDIST, ROCKDENS, DEBRIS, SURFTEMP and POND, correctly classified 64.0 % ($n = 209$) of the locations. Significance of the discriminant function (eigenvalue = 0.16, $\Lambda = 0.86$, p-value < .0001) and model performance (correct classification = 63.0 %) was consistent across all combinations of variable retention. Univariate ANOVAs determined that SOLRAD ($F = 0.0$), SHRUBDIST ($F = 0.01$), ROCKDENS ($F = 0.01$), and POND ($F = 0.01$) had the greatest discriminant ability, whereas SURFTEMP ($F = 0.03$) and DEBRIS ($F = 0.04$) had the least. Strong positive correlations between original variables and the discriminant function occurred for ROCKDENS ($r = 2.6$), DEBRIS ($r = 2.2$), SOLRAD

($r = 0.1$), and SURFTEMP ($r = 0.1$) whereas SHRUBDIST ($r = -0.5$) and POND ($r = -0.1$) contributed strongly but negatively to group separation. This function can be interpreted as an environmental gradient ranging from sites at greater distances from ponds with dense canopy closure, low ground cover of shrubs, rocks, and debris, and reduced solar radiation and surface temperatures towards sites in close proximity to ponds with low canopy closure, dense shrub, debris, and rock cover as well as high surface solar radiation and surface temperature. Separation along the discriminant function reflects that *H. platirhinos* utilized sites (mean discriminant score = 1.84) with a higher percentage of surface debris and rock cover as well as a closer proximity to both ponds and shrubs (Figure 3.3). What's more, lower canopy closure at these locations resulted in greater solar radiative emissivity and concomitant higher surface temperatures.

Parameters retained in the final logistic regression model were identical to those used in the DA, which included: SOLRAD ($ß = 0.05$, $SE = 0.01$, $p < 0.0001$), SHRUBDIST ($ß = -0.42$, $SE = 0.16$, $p = 0.004$), ROCKDENS ($ß = 2.24$, $SE = 0.85$, $p = 0.009$), DEBRIS ($ß = 1.98$, $SE = 0.90$, $p = 0.03$), SURFTEMP ($ß = 0.04$, $SE = 0.02$, $p = 0.03$), and POND ($ß = -0.003$, $SE = 0.001$, $p = 0.0004$). The equation indicated that the probability of activity site selection increased for sites that were in closer proximity to shrubs and ponds while providing greater solar radiative emissivity, surface temperature, as well as rock cover and debris cover ($\chi^2 = 56.27$, $p < 0.0001$).

Visual comparisons indicated that habitat selection varied seasonally. Selected habitat for each season included cleared habitat during the breeding/nesting season (27.3% of breeding/nesting locations) and beech/oak/hardwood during the non-breeding and hibernation seasons (46.7 % of non-breeding locations, 50.0 % of hibernation locations) (Figure 3.4).

Thermoregulation A total of 155 body temperatures (T_b) and 1531 environmental temperature (T_e) measurements were included in the analyses. Snake T_b ranged from 12.2 to 40.9° C (25% and 75% quantiles = 22.3 – 31.1° C, $\mu = 27.4$° C). The preferred body temperature range (T_{set}) is between 29.0 and 32.0° C (Platte 1969), with 28.2 % of T_b measurements occurring within T_{set} ($d_b = 0$). Total exploitation of available T_e falling within T_{set} was 8.8%. ANOVA results indicated that mean T_b did not differ between habitat types ($F_{1,153} = 1.13$, $p = 0.30$), a result that may be attributable to the coarse habitat classification. Operative environmental temperatures (T_e) ranged from 6.3 to 59.5° C ($\mu = 19.7$° C) throughout all habitats and from 10.5 to 33.0° C ($\mu = 24.6$° C) in used habitats. Utilization was highest in forest (69.7 %) whose average T_e (17.6° C) and variability ($\sigma = 6.3$) ranked lower than those experienced in early-successional and developed habitats (18.9° C, $\sigma = 16.3$; 22.5° C, $\sigma = 74.9$ respectively).

Preferred T_e occurred in all three habitat types, with the greatest percentage occurring in developed areas (29.7 %). Of the T_e measurements deviating from T_{set}, critical temperatures were exceeded in early successional ($T_e < 7.0$° C) and developed ($T_e > 40.5$° C) habitats. In contrast, forests maintained T_e within critical limits suggesting that these habitats afforded a permanent refuge from extreme temperatures. Using mean d_e as the metric of thermal quality, early-successional habitat ($d_e = 5.3$) was higher than both developed ($d_e = 5.6$) and forest habitat ($d_e = 8.7$) as it deviated the least from T_{set}. Resultant effectiveness of thermoregulation (E) differed significantly by habitat type ($F_{1,153} = 8.45$, $p = 0.004$) with snakes exhibiting greater levels of thermoregulatory precision in forests ($E = 5.0$) than in developed ($E = 1.9$) or early-successional habitats ($E = 1.9$). Accordingly, activity-site selection for this *H. platirhinos* population was strongly influenced by thermal quality with homogeneous thermal conditions being of greatest importance.

Habitat Model Results and Evaluation

The D^2 values for the study area generated by the Mahalanobis distance model ranged from 1.36 – 210.50 (Figure 3.5). The cumulative frequency graph of snake location and null model D^2 values indicated that D^2 scores ≤ 14.3 correctly classified the greatest percentage of snake locations (2008 = 96 % and 2007 = 82 %) while being most specific for delineating favorable habitat within the study area (56.6 %) (Figure 3.6). In contrast, only 47.0 % of random locations (null model) were correctly classified as favorable habitat.

PCA results determined that the habitat variables contributing the least to overall variation (eigenvalue = .0002), and thus providing the most information towards suitable habitat delineation, were minimum temperature (eigenvalue = .4290) and land cover diversity (eigenvalue = .3838). Variability contributing to misclassification was predominantly attributed to the habitat variables slope (eigenvector = 0.44207), maximum temperature (eigenvector = 0.44057), and elevation (eigenvector = 0.41332), accounting for 66.2 % of total variation among utilized sites (eigenvalue = 4.6335).

Habitat suitability identified by the model was ranked either favorable ($D^2 \leq 14.3$) or unfavorable ($D^2 > 14.3$). Favorable habitat encompassed a total of 674.3 ha and was associated with mixed forest and hemlock cover types (55.0 % total area) (Figure 3.7). These habitat areas occurred at elevations ranging from 118.9 to 400.0 m primarily on chatfield-hollis soil series (32.9 %). Terrain was characterized as being low gradient (0 - 29°) ranging in aspect from 0 to 359° with the majority of the area facing the southeast. Minimum mean surface temperatures ranged from -2.6 – 1.8° C whereas maximum mean surface temperatures ranged from 6.5 – 29.6° C.

Table 3.1. Total captures of *H. platirhinos* during 2007 and 2008 on NBAS, NH. Snake IDs superscripted with asterisks denote individuals utilized in landscape and home range analyses.

Capture Date	Snake ID	Age Class[1]	Sex	Weight (g)	TBL (cm)	# Relocations
May 2007	H014*	adult	F	410	78 (SVL)	8
May 2007	H002*	adult	F	unknown	unknown	22
May 2007	H015	adult	F	280	74 (SVL)	10
May 2007	H023	juvenile	unknown	40	30 (SVL)	1
June 2007	H024*	adult	F	740	85	15
June 2007	H025*	adult	F	240	56 (SVL)	34
June 2007	H001*	adult	F	540	74 (SVL)	19
June 2007	H026*	adult	M	300	58 (SVL)	18
June 2007	H027*	adult	F	660	72 (SVL)	4
June 2007	H029	juvenile	M	53	38	1
June 2007	H028	juvenile	M	80	41 (SVL)	1
July 2007	H030*	adult	F	410	69[2]	6
April 2008	H015*	adult	F	440	85.0	3
May 2008	H026*	adult	M	470.0	58.0	45
May 2008	H040*	adult	F	390.0	72.0	42
May 2008	H041*	adult	F	450.0	85.0	14
June 2008	H042*	adult	F	700.0	100.0	15
June 2008	H043*	adult	M	360.0	31.0	34
July 2008	H044*	adult	unknown	220.0	74.0	2
July 2008	H0J1	juvenile	unknown	100.0	38 (SVL)	1
July 2008	H045*	adult	M	200.0	57.0	26
July 2008	H0J2	juvenile	unknown	125.0	35 (SVL)	1
August 2008	H0A1	adult	F	unknown	78.0	3
Sept 2008	H0H1	hatchling	unknown	unknown	8.0	1
Sept 2008	H0H2	hatchling	unknown	unknown	12.0	1
Sept 2008	H0A2	adult	unknown	unknown	70.0	2

[1] Age classes defined as follows: hatchling 6-10.0 g; juvenile 10-100 g; adult > 100 g.

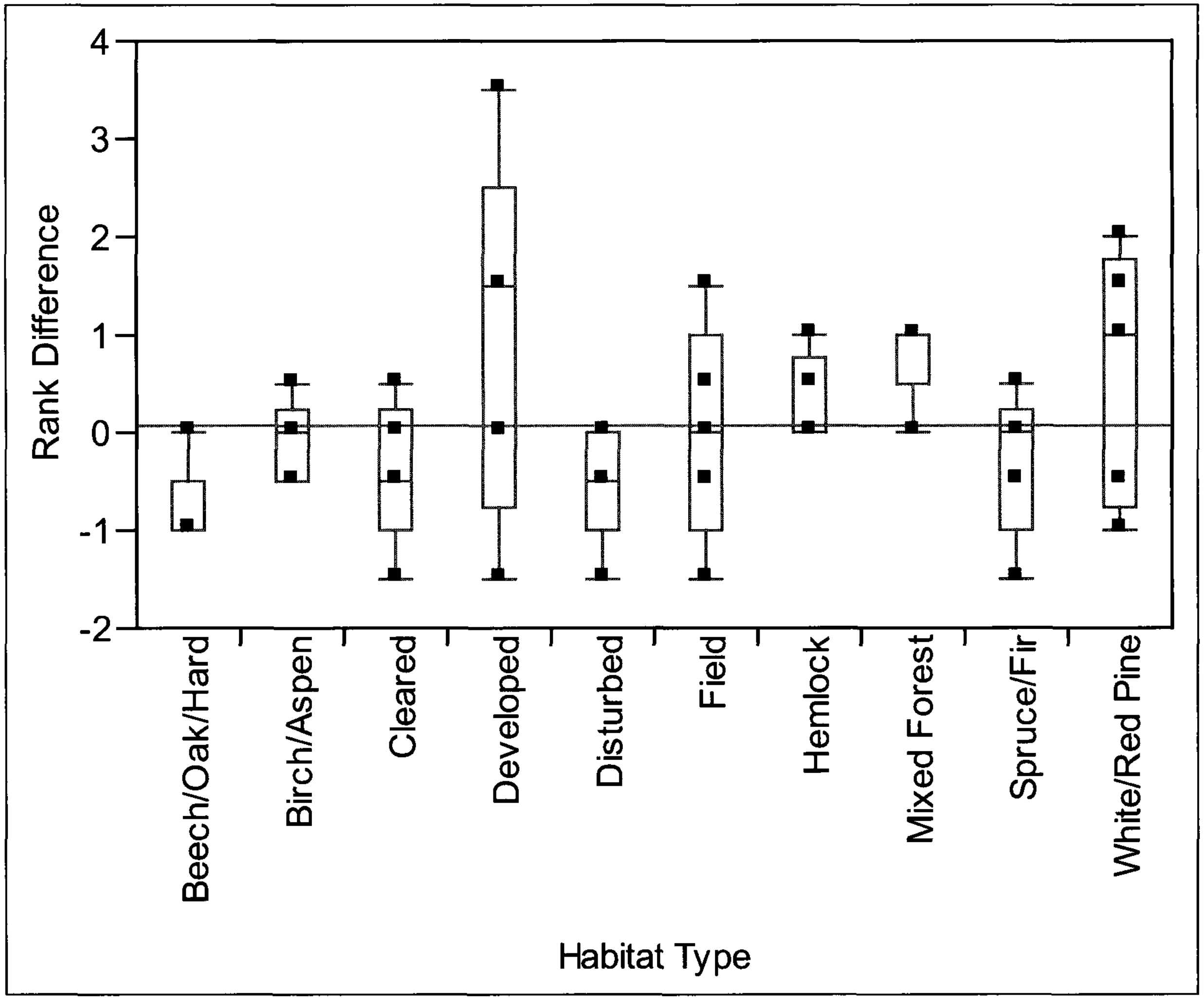

Figure 3.1. Habitat selection at the landscape scale among all *H. platirhinos* individuals on the NBAS in 2008. Positive and negative rank values indicate preference and avoidance, respectively. Horizontal line represents the grand mean (0.07). Boxes denote 25 - 75th percentile range with whiskers extending between the 10th and 90th quantile.

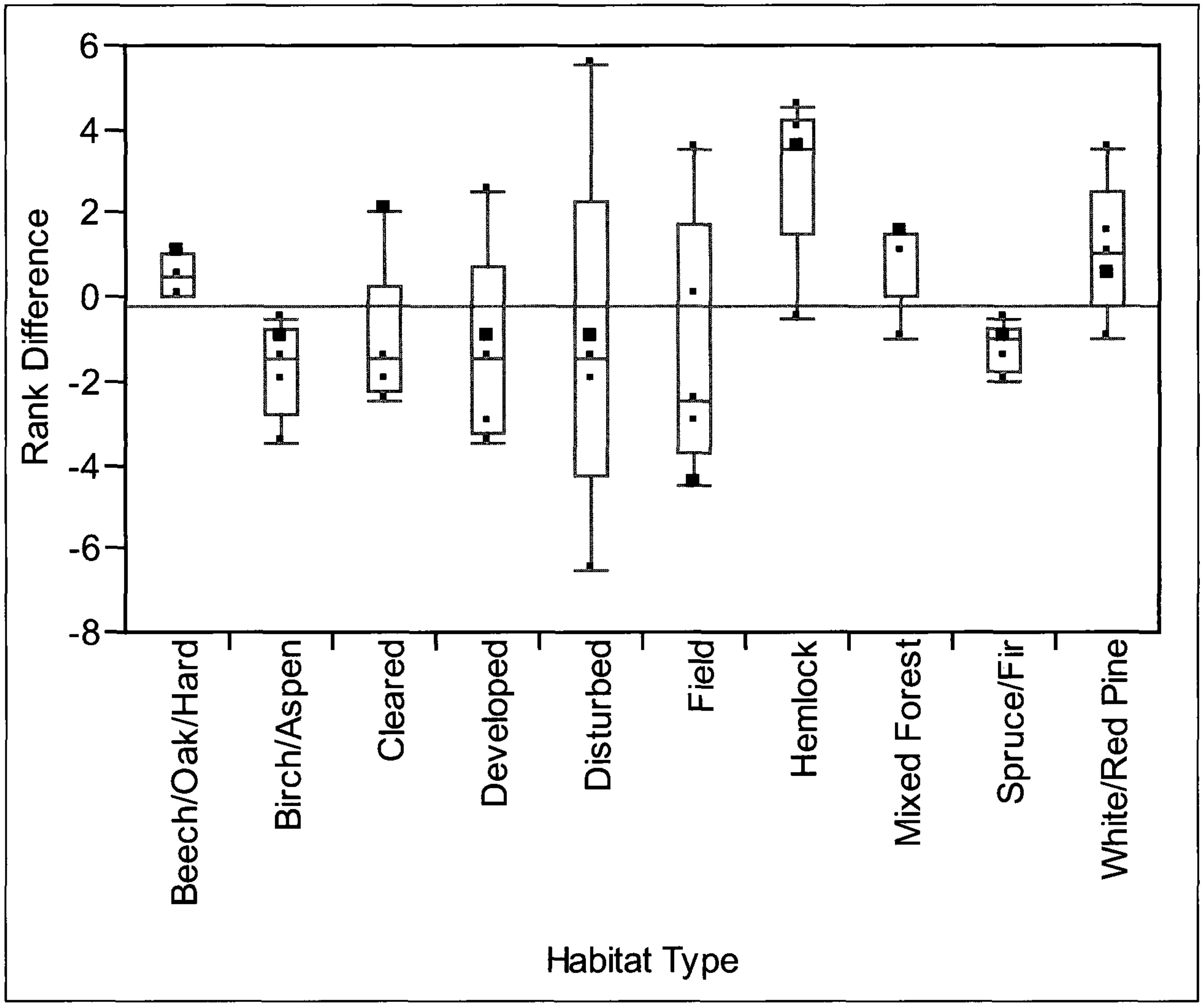

Figure 3.2. Habitat selection at the home range scale among *H. platirhinos* individuals on the NBAS in 2008. Positive and negative rank values indicate preference and avoidance, respectively. Horizontal line represents the grand mean (0.2). Boxes denote 25 - 75th percentile range with whiskers extending between the 10th and 90th quantile.

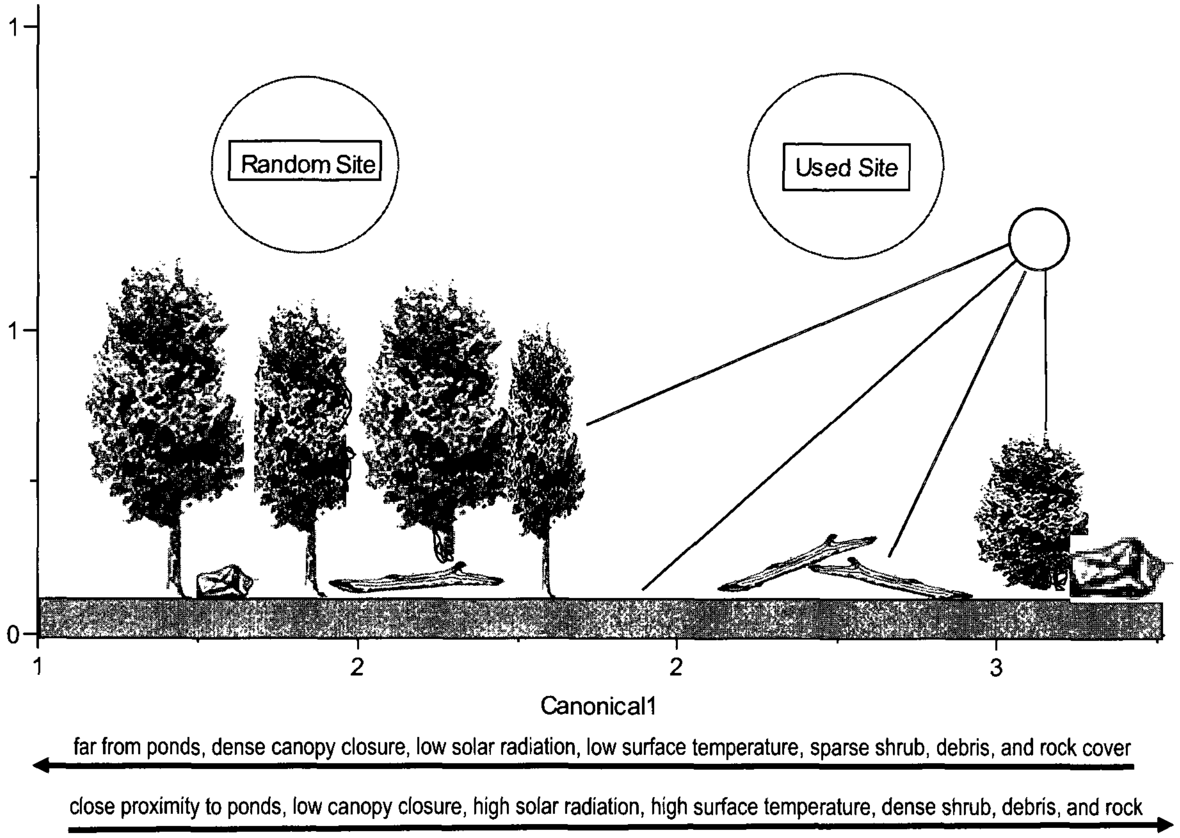

Figure 3.3. Positions of group centroids of used and random locations by *H. platirhinos* on the single discriminant axis at NBAS, 2008. Pictorial interpretation of associated environmental gradients depicts a habitat structure progressing from sites at greater distances from ponds with dense canopy closure, low ground cover of shrubs, rocks, and debris, and reduced solar radiation and surface temperatures towards sites in close proximity to ponds with low canopy closure, dense shrub, debris, and rock cover as well as high surface solar radiation and surface temperature.

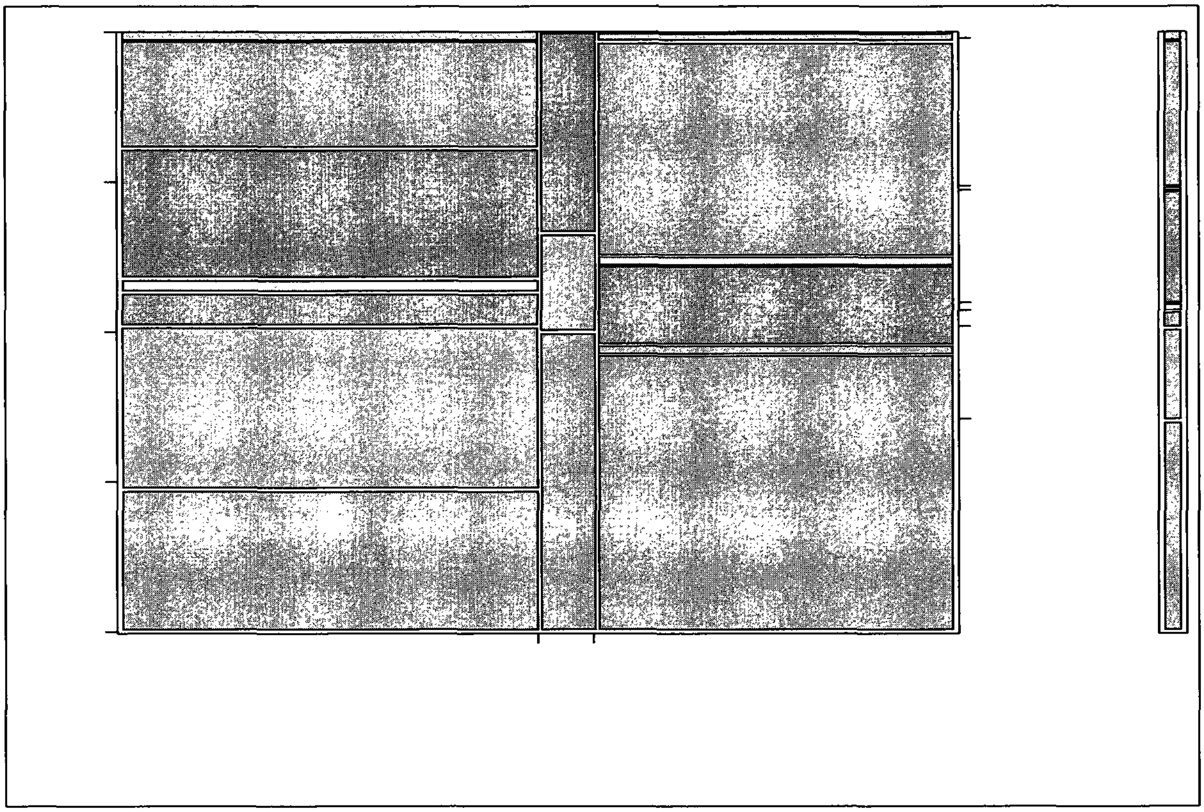

Figure 3.4. Seasonal comparison of habitat selection by *H. platirhinos* at the activity site scale. Percent use of each habitat during the breeding, hibernation, and non-breeding seasons is indicated in each rectangle of the mosaic plot.

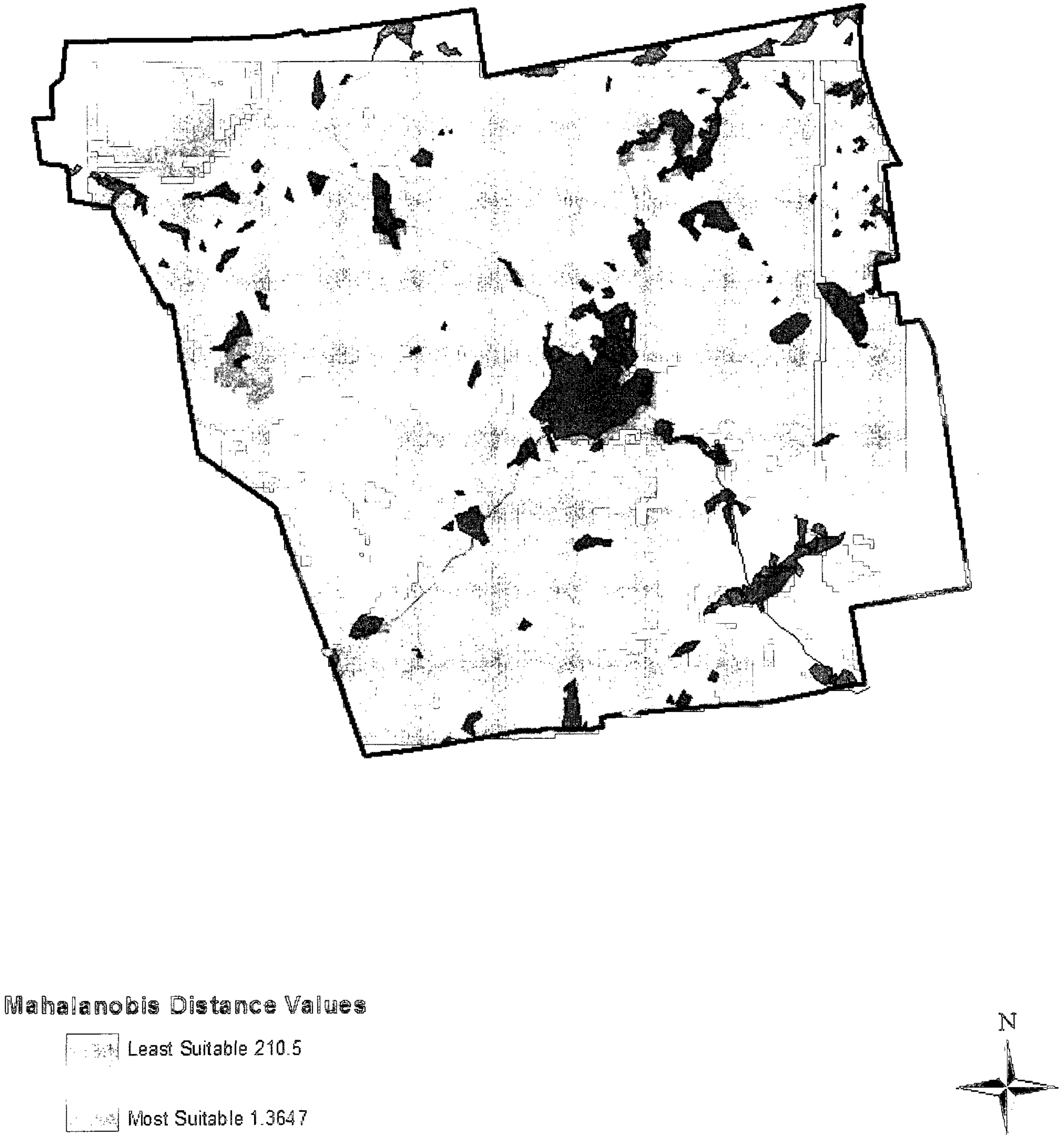

Figure 3.5. Mahalanobis distance (D^2) surface grid characterizing the magnitude of similarity of each pixel to 150 *H. platirhinos* locations on the NBAS, 2008. Similarity was based upon minimum surface temperature and land cover diversity, where habitat suitability values decreased with increasing similarity to known snake locations.

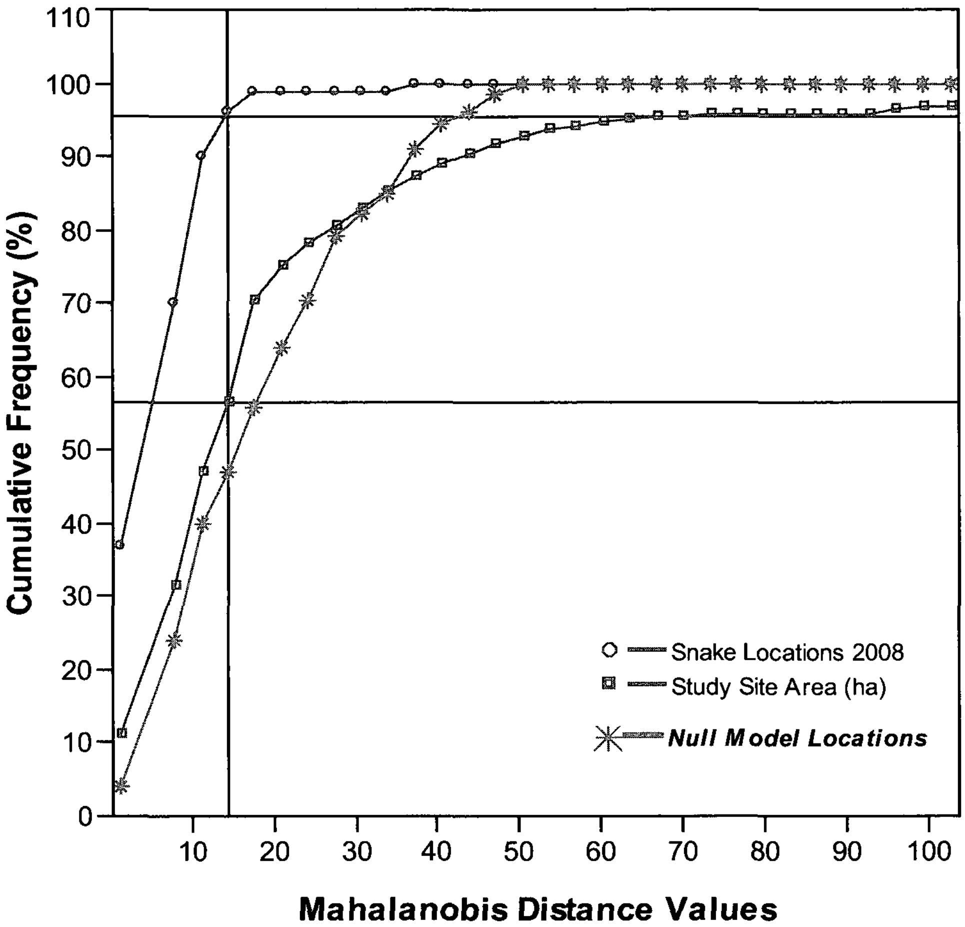

Figure 3.6. Cumulative frequency distribution of Mahalanobis distance values of 150 *H. platirhinos* locations and 150 random locations on the NBAS, 2008. The D^2 threshold value (14.3) was selected by maximizing the predictive gain of the model.

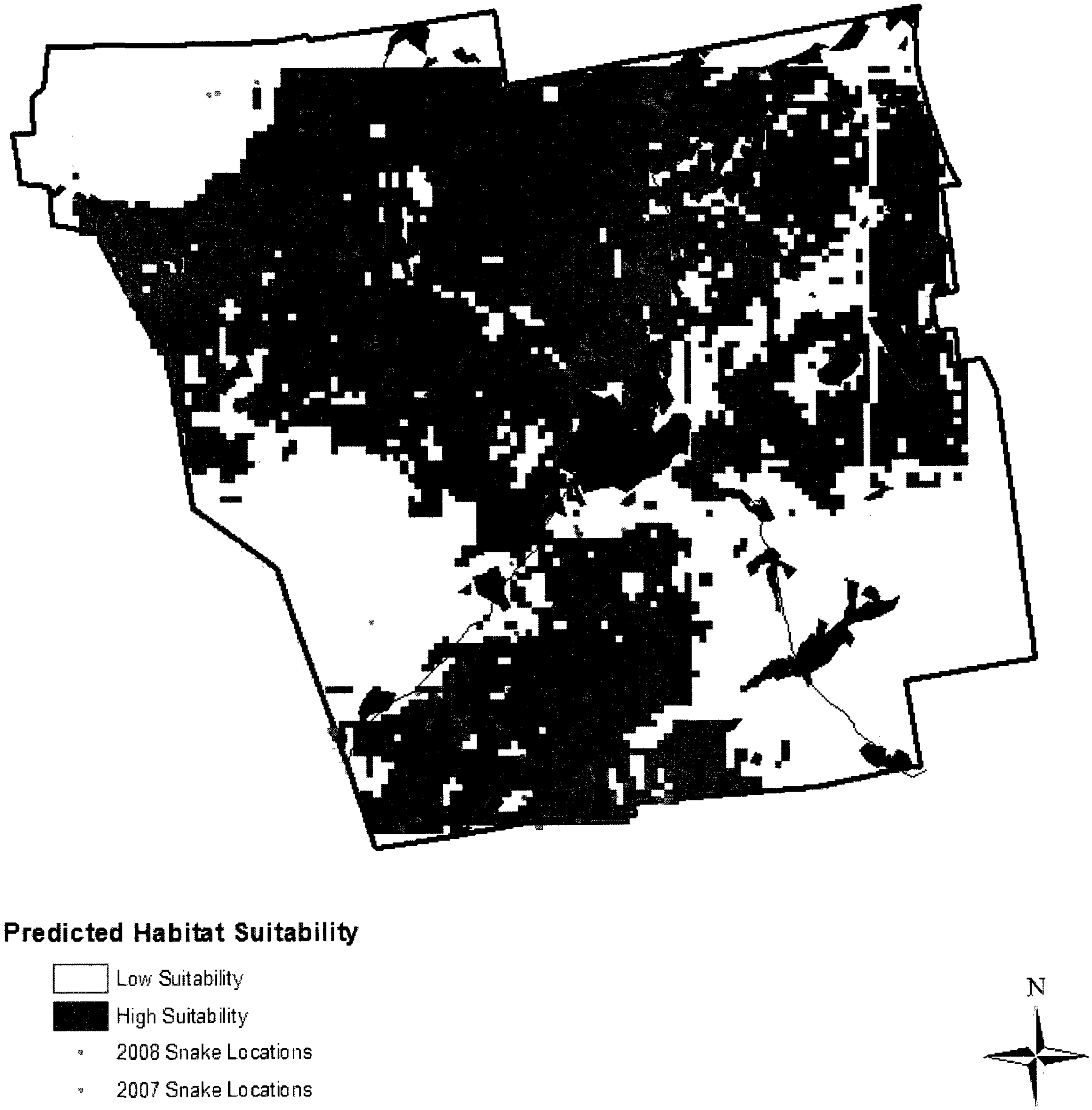

Figure 3.7. Map of favorable *H. platirhinos* habitat within the NBAS (2008) delineated using the D^2 habitat model. Areas in dark green indicate higher potential suitability of habitat whereas light green denotes lower probability of suitable habitat.

CHAPTER 1V

DISCUSSION

Multi-scale Habitat Selection

Landscapes are structured into a hierarchal configuration of habitat patches by the complex interaction of biotic and abiotic variables. Species respond to this scalar environment by selecting habitat, where proximate cues are used to discriminate among the alternative patches. As the magnitude of selective influence imposed by each variable is scale-specific, those exerting the greatest limit on fitness dictate habitat selection patterns at the broadest spatial scales, whereas less critical variables dominate finer scale of selection (Rettie and Messier 2000; McLoughlin et al. 2004). Such influential variables vary across the taxonomic spectrum where each species selects habitat within the confines of its own inherent ecological and physiological requirements.

As ectothermic organisms, habitat selection in snakes is mechanistically linked to fitness through temperature-dependent performance (Row and Blouin-Demers 2006). Given that egg development, growth, hibernation, and ultimate long-term viability are all reliant upon the selection of habitat promoting the maintenance of optimal thermal preferenda to be maintained, the thermal environment has thus been widely considered the key agent driving the hierarchal selective process (Webb and Shine 1998; Moore and Gillingham 2006; Row and Blouin-Demers 2006; Blouin-Demers and Weatherhead 2008). However, as environmental temperatures manifest from the integration of solar radiation, landforms, vegetation structure, and soil type, these variables may also contribute to the selection process as well. This thermally-induced pattern of selective influence was demonstrated by the NBAS population of *H. platirhinos*, where thermal quality and its ecological determinants were identified as the critical variables governing habitat selection at all three spatial scales, with landscape selection being the mildest. Of particular importance were thermal extremes, whereby both broad and fine scale variables affording homogeneous thermal conditions within this species' critical limits were preferentially selected.

At the landscape scale, minimum temperature and habitat type served as the greatest limiting factors constraining *H. platirhinos* distribution. These thermal minima are determined primarily by broad ecological variables, where habitat patch configuration and topography are integral in creating a landscape's thermal regime (Hayden 1998). Drastic horizontal changes in both character and type of vegetation cover interact with the atmosphere to control the magnitude of temperature oscillation (Pielke and Avissar 1990). Topographic properties, including elevation, slope and aspect, further influence minimum temperatures as they dictate both the intensity and duration of radiative inputs incurred upon the landscape. In seeking to minimize erratic climatic fluctuations, analysis and modeling results indicated that selected landscapes were characterized primarily as having mixed forest cover types and a mean elevation of 205 m. Terrain was low in gradient with the majority of the slopes facing the southeast. Together, these structural attributes afforded relatively benign thermal conditions, particularly with respect to minimum temperatures, where surface minima averaged 0.7° C. In contrast, the more thermally extreme beech/oak/hardwood forests were highly avoided as their environmental temperatures fluctuated from -20.5 to 47.5 °C, well below the critical minimum (7.0° C) of this species (Platte 1969).

The magnitude with which thermal extremes proved critical to landscape-scale selection by *H. platirhinos* may be attributable to this population's northern geographic situation. Severe climatic conditions within such thermally challenging environments act to constrain snakes' overall distribution either directly through temperature-induced mortality or indirectly by reduced reproductive success and energy assimilation as a function of activity season constriction (Harvey 2006). Accordingly, *H. platirhinos* landscape distribution encompassed habitats that ameliorated the effects of excessive cold particularly during biologically sensitive life stages like hibernation and incubation. Thus, it can be inferred that, consistent with other ectothermic species, limited hibernacula and nest site availability may be the primary mechanism operating on broad scale habitat selection in this northern population of *H. platirhinos* (Porter et al. 2002, Harvey and Weatherhead 2006).

At finer spatial scales, the more ephemeral thermal maxima emerged as the prevalent selective influence. Expression of these maximum temperatures arises from the more subtle local variability in climatic fluctuations and habitat structure. Seasonal as well as diurnal cycles of air temperature and solar radiative inputs interact with the geometric configuration of within-patch vegetation, forming a mosaic of temporally and spatially discrete thermal regimes. *H. platirhinos* responded individualistically to this thermal mosaic by selecting a subset of available habitats with which to establish their home ranges. The resultant habitat composite of each snake's home range afforded a suite of thermal conditions necessary in performing all their biological activities throughout the course of an activity season. Snakes in this study appeared to preferentially selects hemlock forests over all other available habitats in response to their homogeneous thermal quality. With uniformity in both canopy layering and stand spatial arrangement, these forests provided a relatively constant thermal environment, particularly with respect to maximum temperatures, where surface maxima averaged

25.5° C. In contrast, birch/aspen habitat were avoided, as their thermal regime was highly variable, ranging from 1.5 to 59.9 °C, temperatures well exceeding critical maximum (40.5° C) of this species (Platte 1969).

Additionally, prey resources have also been proposed as a source of selective influence at the home range scale. This is particularly true for anurophagus snake species like *H. platirhinos*, whose limited mobility coupled with the ephemeral availability of its prey, would act to constrain home range selection to habitats affording both the appropriate density and size class of food items (Seigel and Collins 1993). Thusly, it was hypothesized that distribution of primary prey resources, namely *B. americanus*, would dictate *H. platirhinos* selection at this spatial scale whereby individual home ranges would coincide with prey habitat. However, with the poor performance of the *B. americanus* Habitat Suitability Model (refer to *Appendix B*), the extent to which prey availability played a role in home range selection on NBAS is yet to be determined.

Within their individual home ranges, snakes perceived the environment at increasingly narrow spatial and temporal resolutions. As variation in the physical configuration of habitat components corresponds to a particular suite of microclimatic conditions, geometric structure and concomitant light intensity served as the key stimuli by which individuals likely responded (Waldron et al. 2006). *H. platirhinos* utilized these static visual cues to remotely assess the absorptive and convective thermoregulatory opportunities available, and ultimately selected activity sites providing a homogeneous thermal regime. Such sites had minimal canopy closure which enabled much of the transmitted light to penetrate onto the ground surface. However, to avoid extreme thermal maxima resulting from such high levels of incident solar radiation, snakes utilized sites with a high availability of refugia in the form of shrubs, leaf litter, herbs, rocks, and debris. In having the simultaneous accessibility of divergent microclimatic opportunities, *H. platirhinos* individuals were capable of effectively maintaining body temperatures within or slightly below their preferred range, with the least deviation occurring above the upper threshold. What's more, the structural complexity and high refugia availability characterizing the selected activity sites also conferred a protective advantage as well, where detection from visually oriented predators was seemingly reduced. Whether the selection of sites having these specific habitat elements was an artifact of thermoregulatory obligation or an anti-predator strategy is still inconclusive. However, similarity in activity-site configurations in response to predatory avoidance has been well documented in several other snake-related studies suggesting that this variable does impinge some level of influence towards the selective process at this scale (Shine 1991, Webb and Whiting 2005).

Activity site selection shifted seasonally with the pattern of habitat use differing between breeding, non-breeding, and hibernation periods. Presumably, such temporal variability was driven by the specific thermal constraints associated with each biological process (e.g., including reproduction, incubation, ecdysis, foraging, digestion, and hibernation), whereby no one habitat patch was capable of affording the entire set of necessary thermal properties to fulfill each process, coupled with latitudinal positioning. To meet its divergent physiologically-induced thermal requirements, while mediating the impacts of severe environmental conditions, this northern population selected habitat types which served to buffer against extreme temperature fluctuations during seasons which were most critical to survival, including nesting and hibernation periods. During the nesting season, open sites were preferentially selected which afforded high solar radiation emissivity as well as close proximity to asphalt, all of which act to promote high soil temperatures required for successful incubation. Without optimal incubation temperatures (23.4 to 26.1° C), it has been demonstrated that the rate of development can be reduced two fold, de-synchronizing hatching and resource availability and, in turn, inhibiting adequate energy acquisition needed for over winter survival (Platte 1969, Siegel and Ford 2001, Harvey 2006). In contrast, hibernacula occurred in beech/oak/hardwood habitats associated with high canopy cover, dense shrub cover, and the presence of large rocks. Selection of such habitat features served to buffer against the extreme temperature fluctuations inherent to temperate zone winters, thereby promoting successful reproduction, incubation, growth, hibernation, and ultimately, long-term survival.

The overall pattern of habitat use demonstrated by this population of *H. platirhinos* differed markedly from that of other populations elsewhere in its geographic range with respect to habitat preferences and spatial distribution. Throughout much of its range, this species is commonly associated with xeric communities characterized as having sparse vegetation and excessively-drained, sandy soils. In sharp contrast to these ecological affinities, the NBAS snakes preferentially selected more mesic, closed-canopied woodlands, namely mixed and hemlock forests. One possible mechanism driving such geographic variability may be that this is a relictual population. Historically, *H. platirhinos* had a continuous eastern range extending from peninsular Florida in the south to New Hampshire in the north. However, with the drastic loss and fragmentation of its primary habitat throughout much of New Hampshire, this peripheral population has become increasingly isolated, relegated to occupying what is thought to be suboptimal areas. This premise is further substantiated in that these snakes have established large home ranges encompassing a much greater areal extent (approximately 80%) than southern populations (Plummer and Mills 2000), a means by which to compensate for apparently low resource availability and habitat quality (Waldron et al 2006). Alternatively, as structural and climatic properties appear to be more relevant to the selection process in snakes than are specific habitat categories, these divergent vegetative communities may actually be equal in suitability despite differing in diagnostic floristic taxa. Thus, irrespective of geographic situation, each *H. platirhinos* individual was responding similarly within its own unique ecological contexts in that selection was based on the availability of critical thermal, prey, and refugia resources rather than anthropogenicaly contrived habitat types.

Thermoregulation

The thermal environment is a dynamic resource in that it fluctuates across both time and space. Reliant upon this transient resource as its primary means of maintaining optimal body temperatures, a snake's ability to effectively thermoregulate is ultimately constrained by the thermal conditions available within the environment (Reinert 1993). On the NBAS, preferred environmental temperatures occurred in all habitat types with thermal quality being the highest within early-successional habitat and lowest in forest habitats. Irrespective of the availability of high quality areas, analysis results indicated that suboptimal thermal habitat was instead selected at a greater frequency by this population. In utilizing sites slightly below their thermal preferences, individuals were forced to rely upon precise thermoregulation in maintaining body temperatures within their preferred range (29 – 32° C).

Given the overriding influence thermoregulation has upon *H. platirhinos* habitat selection, it would seem reasonable to deduce that the highest thermal quality would have been preferentially exploited, as it would have mitigated the physiological costs incurred from this site's highly variable environment with the least time and energetic investment. Such conflicting results may be attributed to a number of reasons. First, selection of suboptimal habitat may have been an artifact of prey availability. As this species' preferred food items are associated with forest community types, utilizing such habitats would potentially offset the negative thermoregulatory implications by reducing energetic costs and predation risk incurred from extensive foraging excursions. Secondly, it may be that this northern population of *H. platirhinos* has a lower preferred temperature range, thus changing the ranking of selected habitat from sub-optimal to optimal with respect to thermal quality. Such intraspecific plasticity in thermal preferenda has been demonstrated in other species, in particular those inhabiting cooler, more thermally challenging environments like this one (Shine and Madsen 1996; Blouin-Demers and Weatherhead 2000; Angilletta et al. 2002). A third possible explanation may be the disproportionate physiological impacts sustained by severe minimum versus severe maximum temperatures. Studies suggest that body temperatures exceeding a species' thermal maxima are more lethal than those falling below thermal minima (Huey and Kingsolver 1993). Consequently, ectothermic organisms are able to maximize fitness to a greater extent by centering thermal preferenda below optimal body temperatures, thereby diminishing the risk of overexposure (Martin and Huey 2008). This strategy appeared to be employed by *H. platirhinos*, as optimal habitats were not fully exploited due to their frequent departures above critical maxima, whereas habitats affording cooler, yet stable, thermal conditions were instead selected.

It should also be emphasized that due to the broad scale assessment of the thermal environment and coarse habitat classification, thermal quality may have been either over- or under-estimated within each of these categories. This is especially true of forested habitats whose internal structural configuration and external boundary effects create fine-scale variability in environmental temperatures that may not have been captured within the analysis. As a result, patches of optimal thermal habitat may have been interspersed among the more dominant lower quality habitat, obscuring the true thermal quality of the forests.

Management Implications

One of the primary constraints plaguing endangered species conservation is the lack of basic biological information (Plummer and Mills 2000). With the constant loss and fragmentation of ecosystems, the ability to model species-habitat relationships and predict occurrence is vital for the successful protection of these imperiled species. This analytical approach is particularly important for *H. platirhinos* whose sparse distribution and fossorial habits make it especially difficult to manage. In mitigating such obstacles, the multivariate model Mahalanobis D^2 has proven highly effective in identifying *H. platirhinos* habitat within the NBAS and determining ecological phenomena which limit its distribution. This technique's predictive strength stems from it being based upon a collection of interactive variables, a necessary element in modeling *H. platirhinos* habitat as its selective process has been shown to be influenced by multiple ecological factors including thermal quality and its structural determinants. Accordingly, model accuracy was highest when minimum environmental temperature, land cover, and topography were all incorporated. In using this full set of variables, generated probability layers identified optimal *H. platirhinos* habitat as having mixed forest and hemlock cover types occurring on relatively level, southeast facing slopes at moderate elevations, characteristics which created an overall high quality thermal environment with respect to thermal extremes.

Employing such a modeling technique beyond the study would require that the thermal environment be predicted on a regional scale. However, as ground surface temperature varies both spatially and temporally, the derivation of spatially explicit thermal data has traditionally proven problematic due to the theoretical complexity and data deficiency (Cunnington 2006). Factors such as the physiography, emissivity, atmospheric effects, and sensor-to-target noise have all contributed to the difficulties in the determination of ground surface temperature at various scales of resolution (Weng et al. 2004). Recent advancements in modeling techniques, however, have led to the development of what is referred to as the hybrid model (Kang 2000). This approach, based on both heat transfer physics and the empirical relationship between air and soil temperature, has been demonstrated to be applicable in predicting spatial heterogeneity of the thermal environment at a variety of spatial scales. Thus, it is conceivable, yet currently untested, that this technique could be incorporated into other ecological models, like a Mahalanobis D^2-based *H. platirhinos* Habitat Suitability Model, which require ground surface temperature as an input variable. Validation and concurrent modifications of this new regional model could be achieved through the use of snake populations occurring elsewhere in the state (e.g., Pembroke).

If such an approach proves effective in its predictive ability, it could provide numerous beneficial applications towards the conservation of *H. platirhinos*. First, the model can be implemented throughout the region in order to predict other potential populations, thereby focusing survey efforts. What's more, these predicted sites could also serve as optimal release sites of captive bred animals from which the wild *H. platirhinos* population could be supplemented. Secondly, as boundaries delineated by climatic criteria do not always coincide with those defined by structural criteria, connectivity among optimal habitat patches cannot be evaluated solely in terms of cover types. Thus, the environmental thermal data must also be incorporated within the modeling framework in order to accurately assess habitat continuity at the organismal level. Third, habitat management can be enhanced by implementing prescriptions which act to restore and maintain the structural features identified as critical by the model, whereby the full array of climatic conditions required by *H. platirhinos* during each biological process are promoted. And lastly, as physiological constraints influence habitat selection of ectothermic species in much the same way, these methods could presumably be expanded to other endangered snake species as well with thermal quality being adjusted according to the focus species.

Conclusions

Hierarchal multi-scale analysis enabled *H. platirhinos* habitat selection to be fully evaluated. This approach revealed the incongruence of selective forces operating at each level of analysis, where distinct, scale-specific variables regulating the selection process were effectively discerned. Overall results suggested that thermal extremes and its ecological correlates were the most influential variables in *H. platirhinos* habitat selection across the hierarchal continuum. Such variables prompted this species to select habitat having structural attributes which translated into an explicit set of climatic conditions, thereby enabling precise thermoregulation to be achieved. Optimal habitat, as revealed by both statistical and model results, had the following characteristics: 1) low elevational clines facing the southeast; 2) mixed and hemlock forests having relatively continuous canopy and understory architecture interspersed with small-scale openings; 3) close proximity to wetlands; and 4) high density of leaf litter, debris, and rocks. Together, this structural configuration provided *H. platirhinos* with adequate thermoregulatory opportunities by way of solar radiative absorption or surface convection while still conferring protection from decimating thermal minima and maxima. In addition to fulfilling thermoregulatory requirements, the secondary biological needs of predator avoidance and potentially prey availability were also satisfied by such selected habitat.

APPENDIX A

MULTI-SCALE HABITAT SELECTION RESULTS

Table A.1. Used and available proportions of ten habitat types for *H. platirhinos* within the landscape range on the NBAS, 2008. Average differences between ratios were calculated and ranked in order of preference with 1 denoting most preferred and 10 denoting least preferred.

	Developed		**Field**		**Beech/ Oak/ Hardwood**		**Birch/ Aspen**		**White/ Red Pine**		**Spruce/ Fir**		**Hemlock**		**Mixed Forest**		**Disturbed**		**Cleared**	
ID	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**	**U**	**A**
H026	0.01	0.02	0.09	0.03	0.22	0.34	0.00	0.00	0.05	0.06	0.00	0.00	0.10	0.09	0.46	0.38	0.00	0.00	0.04	0.03
H040	0.03	0.02	0.02	0.03	0.41	0.34	0.00	0.00	0.03	0.06	0.00	0.00	0.06	0.09	0.32	0.38	0.00	0.00	0.05	0.03
H042	0.00	0.02	0.02	0.03	0.38	0.34	0.00	0.00	0.07	0.06	0.00	0.00	0.07	0.09	0.36	0.38	0.00	0.00	0.03	0.03
H043	0.00	0.02	0.06	0.03	0.34	0.34	0.00	0.00	0.03	0.06	0.01	0.00	0.07	0.09	0.33	0.38	0.01	0.00	0.05	0.03
H045	0.00	0.02	0.02	0.03	0.51	0.34	0.00	0.00	0.10	0.06	0.00	0.00	0.04	0.09	0.29	0.38	0.00	0.00	0.02	0.03
Mean D	1.0		0.0		-0.8		-0.1		0.6		-0.3		0.3		0.8		-0.5		-0.4	
Rank	1		5		10		6		3		7		4		2		9		8	

Table A.2. Used and available proportions of ten habitat types for *H. platirhinos* within the home range on the NBAS, 2008. Average differences between ratios were calculated and ranked in order of preference with 1 denoting most preferred and 10 denoting least preferred.

	Developed		**Field**		**Beech/ Oak/ Hardwood**		**Birch/ Aspen**		**White/ Red Pine**		**Spruce/ Fir**		**Hemlock**		**Mixed Forest**		**Disturbed**		**Cleared**	
ID	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**	**o**	**π**
H026	0.02	0.01	0.51	0.09	0.21	0.22	0.00	0.00	0.02	0.05	0.00	0.00	0.00	0.10	0.21	0.46	0.00	0.00	0.02	0.04
H040	0.00	0.03	0.00	0.02	0.61	0.41	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.06	0.17	0.32	0.00	0.00	0.22	0.05
H042	0.00	0.00	0.06	0.02	0.25	0.38	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.07	0.63	0.36	0.00	0.00	0.06	0.03
H043	0.00	0.00	0.00	0.06	0.46	0.34	0.00	0.00	0.00	0.03	0.00	0.01	0.00	0.07	0.09	0.33	0.11	0.01	0.09	0.05
H045	0.00	0.00	0.69	0.02	0.23	0.51	0.00	0.00	0.04	0.10	0.00	0.00	0.00	0.04	0.04	0.29	0.00	0.00	0.00	0.02
Mean D	-1.3		-1.3		0.5		-1.7		1.1		-1.2		3.0		0.9		-1.1		-1.1	
Rank	9		8		4		10		2		7		1		3		5		6	

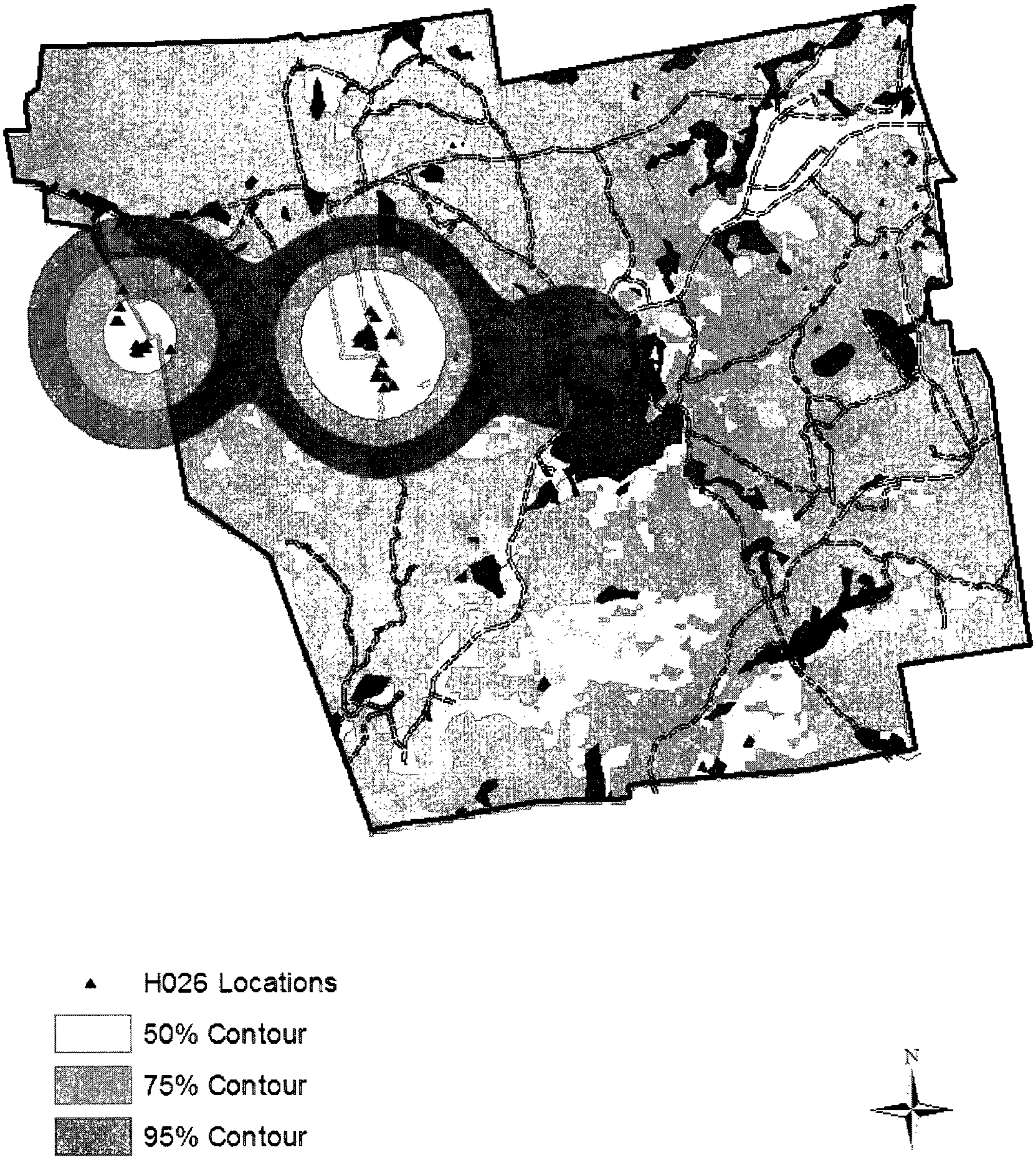

Figure A.1. Map depicting snake locations and home range estimation of *H. platirhinos* H026 in 2008.

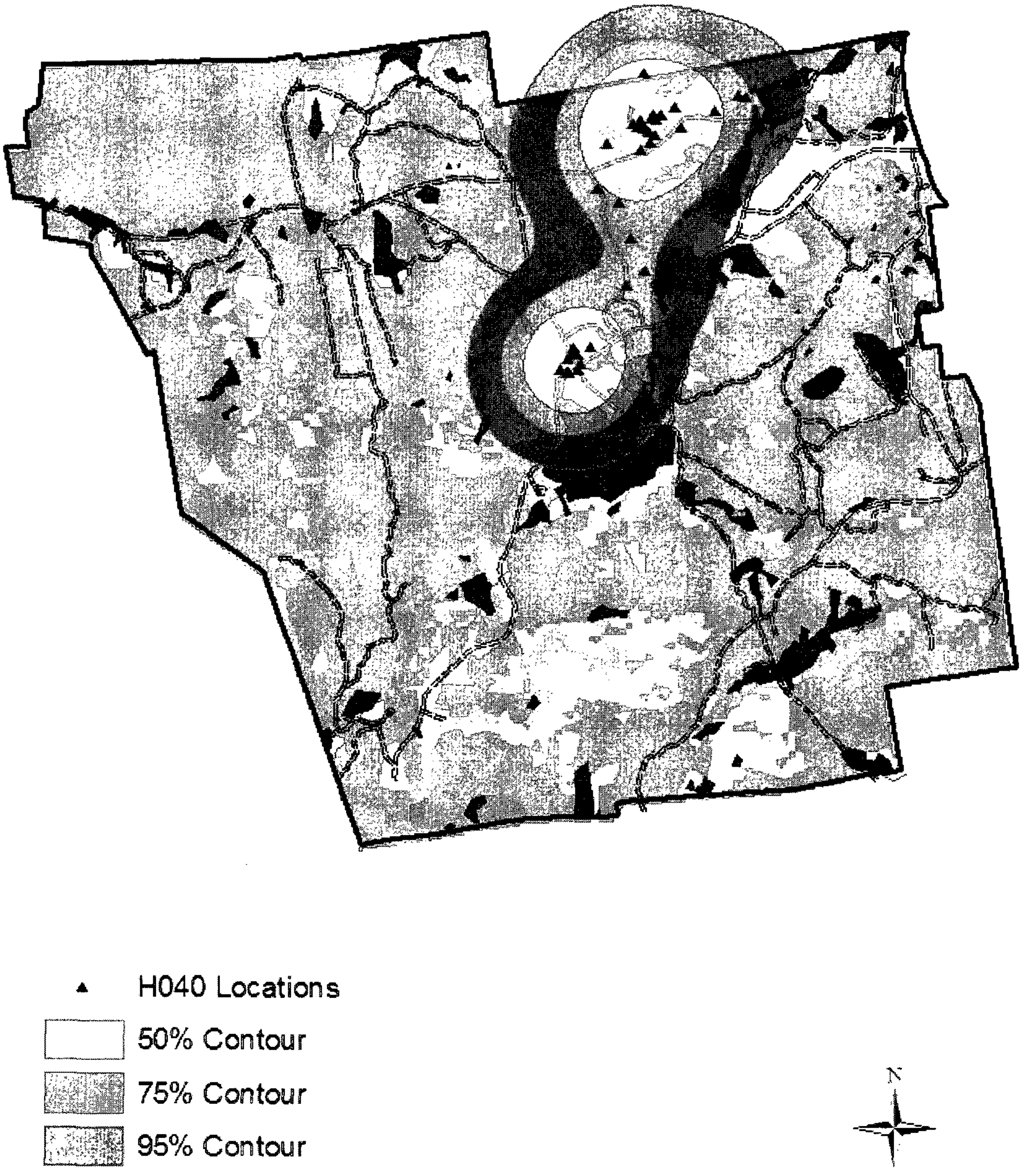

Figure A.2. Map depicting snake locations and home range estimation of *H. platirhinos* H040 in 2008.

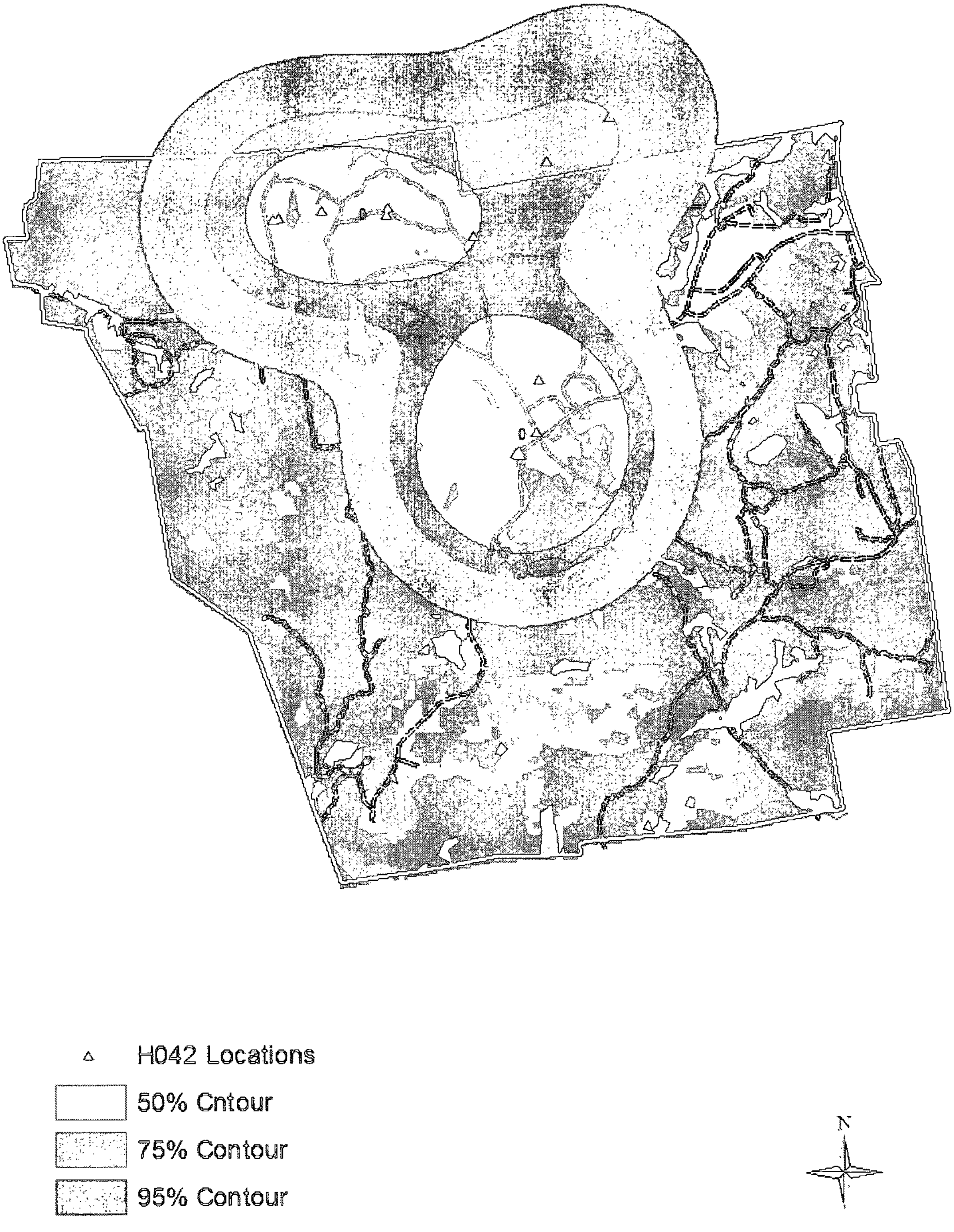

Figure A.3. Map depicting snake locations and home range estimation of *H. platirhinos* H042 in 2008.

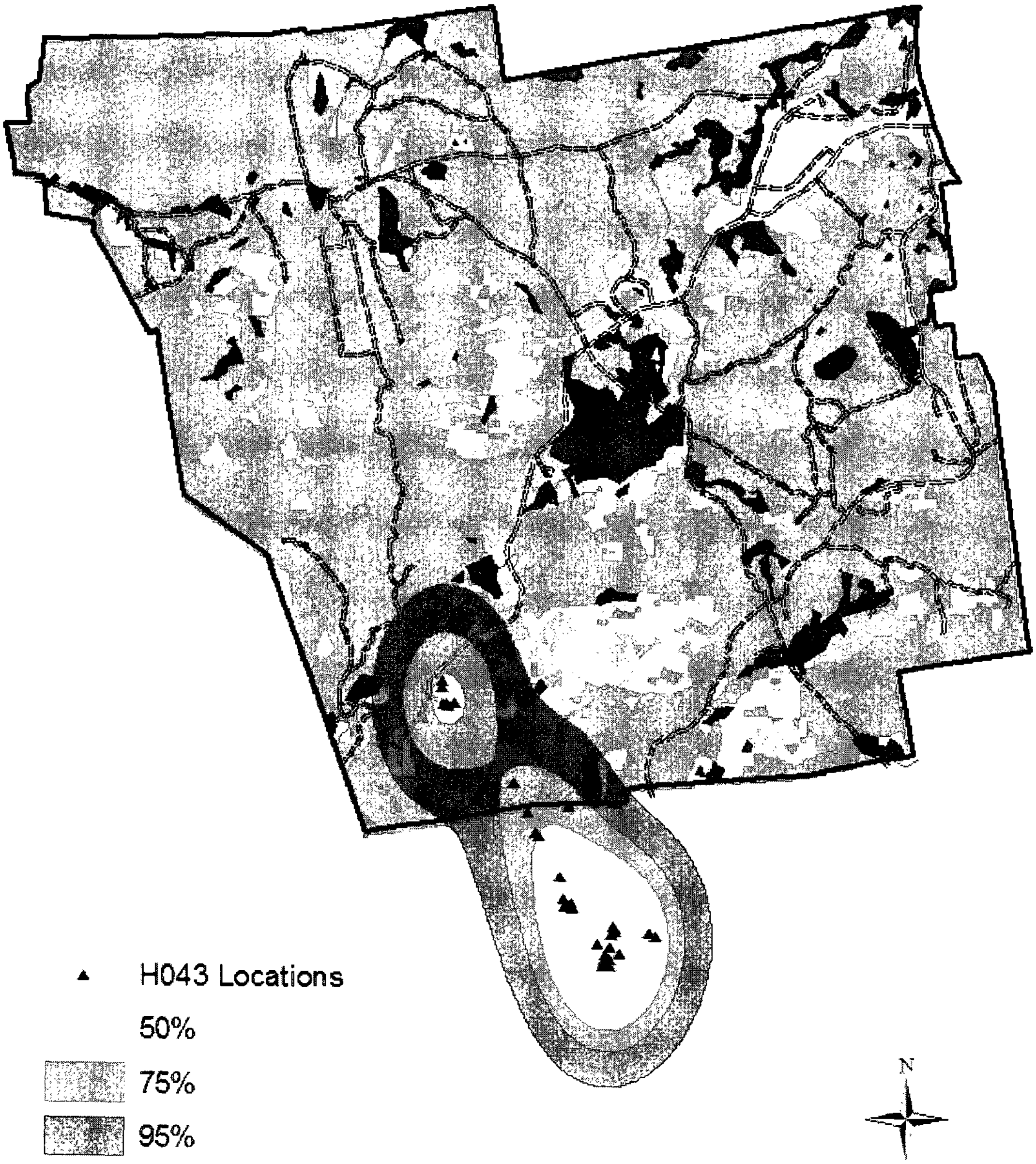

Figure A.4. Map depicting snake locations and home range estimation of *H. platirhinos* H043 in 2008.

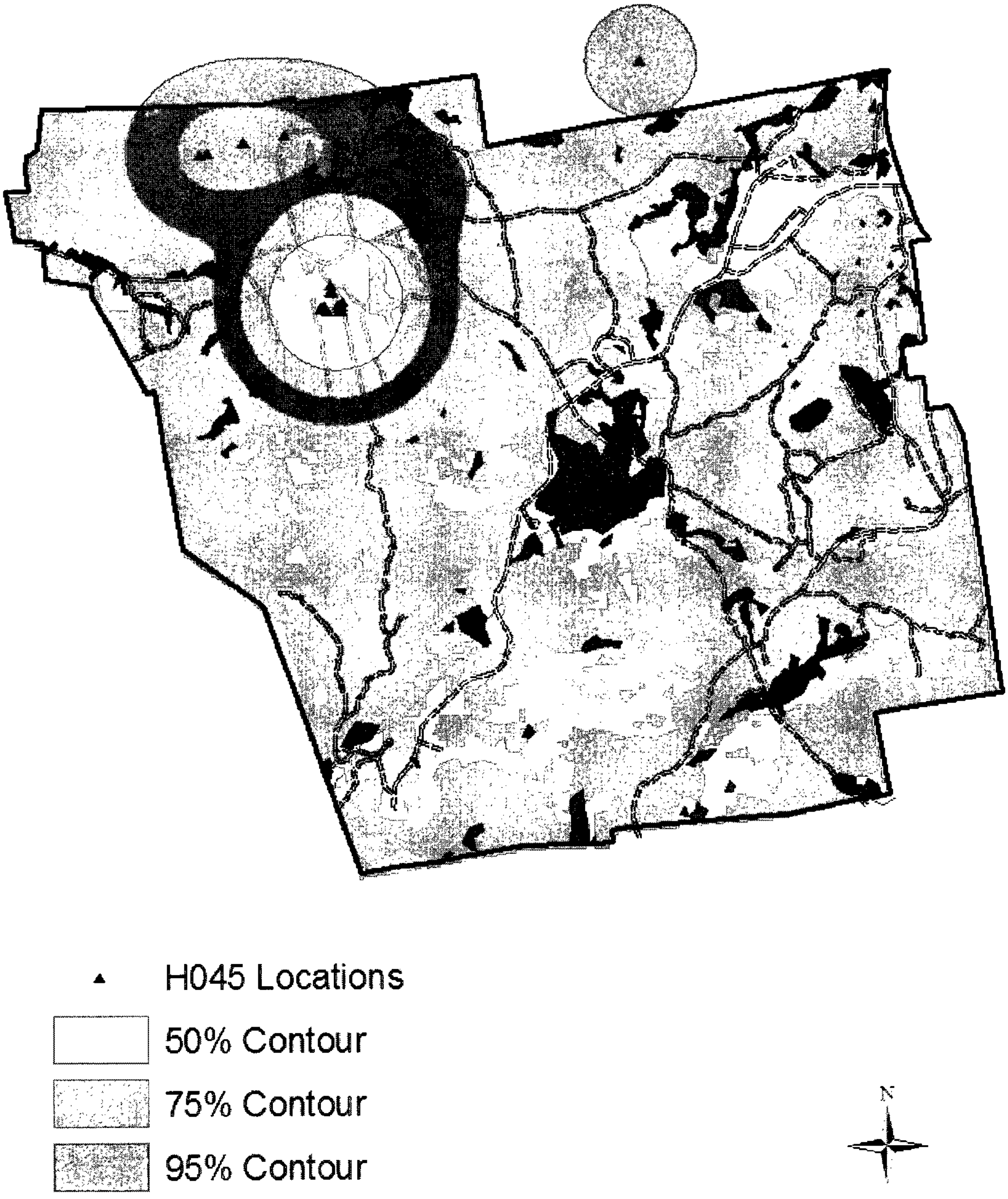

Figure A.5. Map depicting snake locations and home range estimation of *H. platirhinos* H045 in 2008.

APPENDIX B

PREY HABITAT SUITABILITY MODEL

Model Development

A habitat suitability model was developed for *H. platirhinos*' primary prey item *Bufo americanus*. Model development was based on variables important to species distribution during both breeding and non-breeding seasons using land cover, soil survey, wetland, and NBAS boundary spatial layers. Variables included wetland type, wetland size, hydroperiod, upland land cover, and soil type. Suitability values were assigned to each based on literature reviews of habitat associations for *B. americanus* (Table B.1). Pixel values for each habitat suitability variable were reclassified from 1 to 3 in ArcMap 9.0 (Environmental Systems Research Institute, Inc., Redlands, CA, USA), with higher numbers corresponding to greater suitability. GIS layers for each reclassified habitat variable were multiplied using Spatial Analyst to create breeding and non-breeding landscape maps, with variables for each being analyzed separately. Suitability categories ranged from Low to High and were assigned according to the combined scores of each habitat variable. Non-breeding habitat was delimited by the average toad dispersal distance of 1500 m buffer around each predicted breeding pond. The two habitat maps were then reclassified into five categories ranging from Very Low to Very High suitability to create a final map depicting predicted breeding and non-breeding habitat (Figure B.1). Available prey density within snake home ranges was then determined by overlaying the prey distribution map with individual fixed-kernel estimates. Predicted prey densities were based on predicted habitat quality where high suitability values corresponded to high densities and low suitability values corresponded to low densities.

Wetland Type Wetland type is one of the most significant variables influencing *B. americanus* presence (Knutson et al. 1999). As this species prefers shallow, warm waters, wetlands characterized as marshes are particularly important for toads (Houlahan and Findlay 2003). Wetlands coded as marsh were, therefore, assigned the highest suitability while all others received lower rankings.

Wetland Size and Hydroperiod Variation among anuran life history traits results in species-specific patterns of distribution among breeding sites that are largely driven by wetland permanence and pool size (Babbit 2005). Both of these characteristics influence wetland use as they are strongly correlated with each species' own unique development rate as well as susceptibility to predation. Metamorphosis of *B. americanus* occurs over a relatively short period of time, eliminating the time constraint imposed by hydroperiod (Halley et al. 1996). In addition, unlike many other anuran species, *B. americanus* is able to persist in pools large enough to support fish, as their tadpoles are not vulnerable to fish predation (Halley et al. 1996). As the increased presence of predators in larger, more permanent wetlands precludes the establishment of competing anuran species, *B. americanus* tends to select such sites. Accordingly, large size class wetlands (> 2 ha) having intermediate hydroperiods were ranked highest.

Land Cover The proportion of forest surrounding a wetland is critical to several anurans, particularly for highly terrestrial species like *B. americanus*. Forests serve to buffer wetlands against changes in water quality and hydroperiod, both of which strongly influence larval growth, survival, and community structure (Burne and Griffin 2005; Otto et al. 2007). In addition, forest cover serves to provide refugia and dispersal corridors during the non-breeding and over-wintering seasons. These corridors are especially vital to juveniles who tend to avoid open canopy habitat while dispersing to neighboring wetlands, without which population connectivity would not be maintained. As such, deciduous forests characterized by dense litter were assigned a high ranking and non-forested areas were ranked low.

Soil Characteristics Soil properties influence the distribution of many anuran species (Dayton and Fitzgerald 2006). *B. americanus* is a fossorial species that requires loose, sandy soils with some organic matter in order to burrow. Such characteristics facilitate excavation as well as afford moist refuges to prevent desiccation. Soils ranging from loam to fine-sandy-loam received higher ranks while coarse-rocky soils were ranked low.

Wetland Buffer Proximity to forested uplands from wetlands is positively related to occupancy by *B. americanus* (Cushman 2006). It has been demonstrated that most adults disperse between 400 and 1000 m from the breeding pond, whereas juveniles may utilize forested habitat extending up to 1.5 km from the breeding site (Forester et al 2006). Therefore, a 1.5 km buffer surrounding each predicted breeding pond was given a high suitability ranking and areas outside the buffer were assigned a low ranking.

Model Evaluation

To validate the *B. americanus* model, 12 ponds (3 Low, 6 Medium, and 3 High) identified by the model as breeding habitat were selected as survey sites. Site selection was constrained by accessibility and logistical issues resulting in uneven sampling effort between habitat categories. Aural surveys for the presence of *B. americanus* were conducted in late April. A total of 12 wetlands were surveyed throughout NBAS. Wetlands ranged from .02 ha to 16.90 ha (mean of 2.01 ha) and encompassed a variety of hydroperiod classifications. Each wetland was surveyed once during the breeding season. Site visits began one-half hour after sunset and consisted of one minute of silence followed by ten minutes of observation. Calling intensity was estimated using the following index: CI of 0 for no calling individuals, 1 for 1–10 individuals, a CI of 2 for 11-35 individuals, and a CI of 3 for >35 individuals (Lepage et al. 1997). In addition to occupancy, GPS location, time of day, air temperature, precipitation, relative humidity, wind velocity, moon phase, and cloud cover were also recorded. GPS locations were recorded using a handheld unit and environmental data were obtained from the New Boston weather station. A map depicting observed *B. americanus* habitat was then generated using the final habitat suitability map. Occupied breeding sites were selected using Spatial Analyst and surrounding non-breeding habitat was delimited by a 1500 m buffer around each of these ponds. Observed prey availability within snake home ranges was then determined by overlaying the prey distribution map with individual fixed-kernel estimates.

The accuracy of the habitat suitability model was evaluated by using the Likelihood Ratio test to examine whether the observed frequency of occurrence in each habitat category was different than would be expected (Dayton 2005). This test is the standard method for evaluating independence among categorical data when sample sizes are small, which was the case with this dataset. Resulting G-values indicate the degree of association, where values approaching 1 would suggest strong predictive ability of model parameters.

Model Results

H. platirhinos prey availability was estimated utilizing the *B. americanus* habitat suitability model and aural survey results based on the premise that density is positively correlated to habitat quality. Model results identified a total of 0 ha of Very Low Prey Density, 0.2 ha of Low Prey Density, 41.9 ha Medium Prey Density, 61.3 ha of High Prey Density, and 303.3 ha Very High Prey Density areas with higher density categories occurring in a scattered distribution throughout NBAS. Predicted prey availability occurred in all five snake home ranges. Total area of all predicted density classes ranged from 74.74 ha to 425.44 ha (μ = 186.75 ha) with percent cover ranging from 41.70 to 83.28 (μ = 61.25%). The predicted High Prey Density class encompassed the largest proportion of area within the home ranges (μ = 112.18 ha) whereas the Predicted Low Prey Density class encompassed the least (μ = 1.82 ha). No overlap occurred between the Predicted Very Low Prey Density and any of the home ranges. Co-occurrence and home range size did not appear to be related in that larger home ranges did not correspond to greater proportion of overlap between home range areas and observed or predicted prey availability.

Aural surveys indicated toad presence at 4 (33%) of the 12 surveyed sites primarily in the southern portion of NBAS. Overall calling indices (CI) ranged from 0 (no calling individuals) to 1 (1-10 individuals) with all occupied ponds having a CI of 1. Such calling indices correlated to an estimated population size of 8 to 80 individuals within the 1500 m dispersal distance of the occupied sites (Nelson and Graves 2004, Stevens and Paszkowki 2004). Spatial overlap between this observed prey distribution and snake home ranges encompassed areas ranging from 14.46 ha (7.14 %) to 146.76 ha

(36.95 %) (Table B.3). Of the four utilized sites, *B. americanus* individuals utilizing the High suitability category occurred at a higher frequency than expected (0.72), however the computed Likelihood Ratio *G*-statistic (4.3) exceeded the critical value for a 0.05 probability level suggesting a low predictive ability of the model (Table B.2).

Discussion

Snake habitat selection at the home-range scale reflects the availability of vital resources, particularly prey. Both foraging behavior as well as dietary preferences has profound affects on the resultant size and distribution of individual home ranges. Due to a suite of physiological traits inherent to many snake species, such as low endurance capacity, short activity season, and high susceptibility to predation, long-distance movements in search of prey is inhibited (Madsen and Shine 1996). Instead, most snakes rely on a sit-and-wait foraging mode. Adequate prey densities, therefore, must occur within selected home ranges to fully satisfy energy requirements throughout the course of the activity season. However, food availability is not simply a function of prey abundance for these gape-limited predators, but of prey size as well. Because snakes consume their prey whole, most species undergo an ontogenetic shift in diet where prey size increases as a function of body growth. Such shifts in diet composition dictate the ultimate configuration of selected home ranges in response to the availability of appropriate size classes of prey.

For anurophagus species like *H. platirhinos*, these physiological and morphological limitations coupled with the ephemeral nature of their primary prey further influences home range selection. *H. platirhinos* diet consists primarily of amphibians, with species of the family Bufonidae being the preferred food item. These primary prey species demonstrate biphasic habitat use of both aquatic and terrestrial systems. During their terrestrial phase, bufoids are associated with a range of habitat types including forests, open fields, and residential lawns, however, deciduous forests characterized by dense litter is utilized most extensively. It follows then, that *H. platirhinos* home ranges would encompass such habitats, in particular, deciduous forests in order to be within close proximity to their prey.

This assumption was well demonstrated from results of the habitat suitability model. Model predictions determined that the majority of the NBAS supported high densities of *B. americanus*, with spatial overlap of these high density categories occurring within all of the snake home ranges. Percent aerial cover of home ranges ranged from 40 to 83 % of total area. Larger females appeared to have a greater cover of predicted high prey densities than the smaller males. These results could be attributed to variation in energetic requirements associated with reproductive condition where breeding females would consume more prey to compensate for the energetic costs of egg production. What's more, female snakes generally have larger body masses than males further adding to their energetic needs.

Aural survey results did not indicate as strong a correlation between prey availability and *H. platirhinos* home range selection. Aerial overlap of observed prey and snake home ranges ranged between 19 % and 37 %, an overall 55 % reduction in co-occurrence from that demonstrated from the habitat suitability model. However, these results should be viewed with caution as surveys results were severely impacted by a number of factors including: 1) timing of surveys; 2) pond selection restrictions; and 3) meteorological conditions. Had surveys been conducted during the peak calling period and at greater number of locations, survey results and model performance may have been improved.

Habitat associated with areas of co-occurrence identified by both model and aural surveys was characterized as being predominantly mixed and beech/oak forests, both of which were highly selected for by *H. platirhinos* at this scale. Such habitat affinities are in stark contrast to those of other populations of *H. platirhinos*. As habitat propensities are strongly influenced by prey availability (Seigel and Collins 1993), difference in primary prey may explain the variation in habitat selection between this peripheral population of *H. platirhinos* and more southern populations. In contrast to New Hampshire populations, the diet of the more southerly occurring *H. platirhinos* is predominantly *Bufo fowleri*, a species which utilizes dry forest communities such as pitch pine and scrub oak barrens. Accordingly, these snake populations also select these more xeric habitat situations.

Nonetheless, model predictions were not substantiated as the model performance was poor. Such low accuracy may be due to three primary issues. First, parameters utilized in model development may not have fully captured minimum habitat requirements of *B. americanus*. Without including the most influential factors controlling habitat use, identifying highly suitable sites is futile. Secondly, this type of modeling is based upon the premise that habitat variables can be assigned a numerical value corresponding to the level of quality. Indices designation is a somewhat arbitrary process which may be biased by our own perceptions and assumptions of suitability.

What's more, this modeling approach assigns equal weights to each parameter while ignoring the interaction among variables. And third, model performance may have been hindered by the nature of the species. As a habitat-generalist, *B. americanus* may not have specific distinguishable habitat affinities, thereby reducing the ability to model toad presence based solely on habitat variables.

Table B.1. Assigned suitability values of habitat variables included in prey model.

Variable	**Low Rank (1)**	**Medium Rank (2)**	**High Rank (3)**
Breeding Habitat Land Cover	Non-Forest	none	Forest
Wetland Type	Lacustrine and Unconsolidated Bottom	Palustrine Scrub-shrub	Palustrine Emergent and Forested
Wetland Size	none	< 2 ha	> 2 ha
Wetland Hydroperiod	none	Temporary	Semi-permanent - Permanent
Non-breeding Habitat Land Cover	*Non-Forest*	Non-deciduous Forest	*Deciduous Forest*
Soil	Stony-Stony Loam	Stony Fine Sandy Loam	Well-drained-Fine Sandy Loam
Distance from Breeding Pond	> 1.5 km	none	≤ 1.5 km

Table B.2. Occurrence of calling male *B. americanus* in each of the three predicted breeding habitat categories.

Predicted Habitat Category	Observed CI in Each Habitat Category	Expected CI in Each Category (%)	Proportion of Individuals in Each Habitat Category
Low	1	1.45	25
Medium	1	1.81	25
High	2	.72	50

Test	Chi Square	P-value
Likelihood Ratio	4.92	.09

Table B.3. Observed and predicted prey availability in each snake home range. Observed prey areas were based on aural surveys whereas predicted areas were based on model results.

	Observed		Predicted						
Snake ID #	Observed Prey Area (ha)	% Cover of Observed Prey	Very Low Prey Density Area (ha)	Low Prey Density Area (ha)	Medium Prey Density Area (ha)	High Prey Density Area (ha)	Very High Prey Density Area (ha)	Total Prey Density (ha)	Total % Cover of Prey
H026	43.32	19.00	0.00	0.00	11.04	92.00	75.27	178.31	78.21
H040	14.46	7.14	0.00	0.02	16.50	129.08	23.00	168.60	83.28
H042	146.76	24.95	0.00	3.80	24.13	281.32	116.19	425.44	72.31
H043	33.40	18.64	0.00	0.00	3.25	58.50	12.99	74.74	41.70
H045	77.98	36.95	0.00	5.27	6.69	0.00	74.68	86.64	30.75

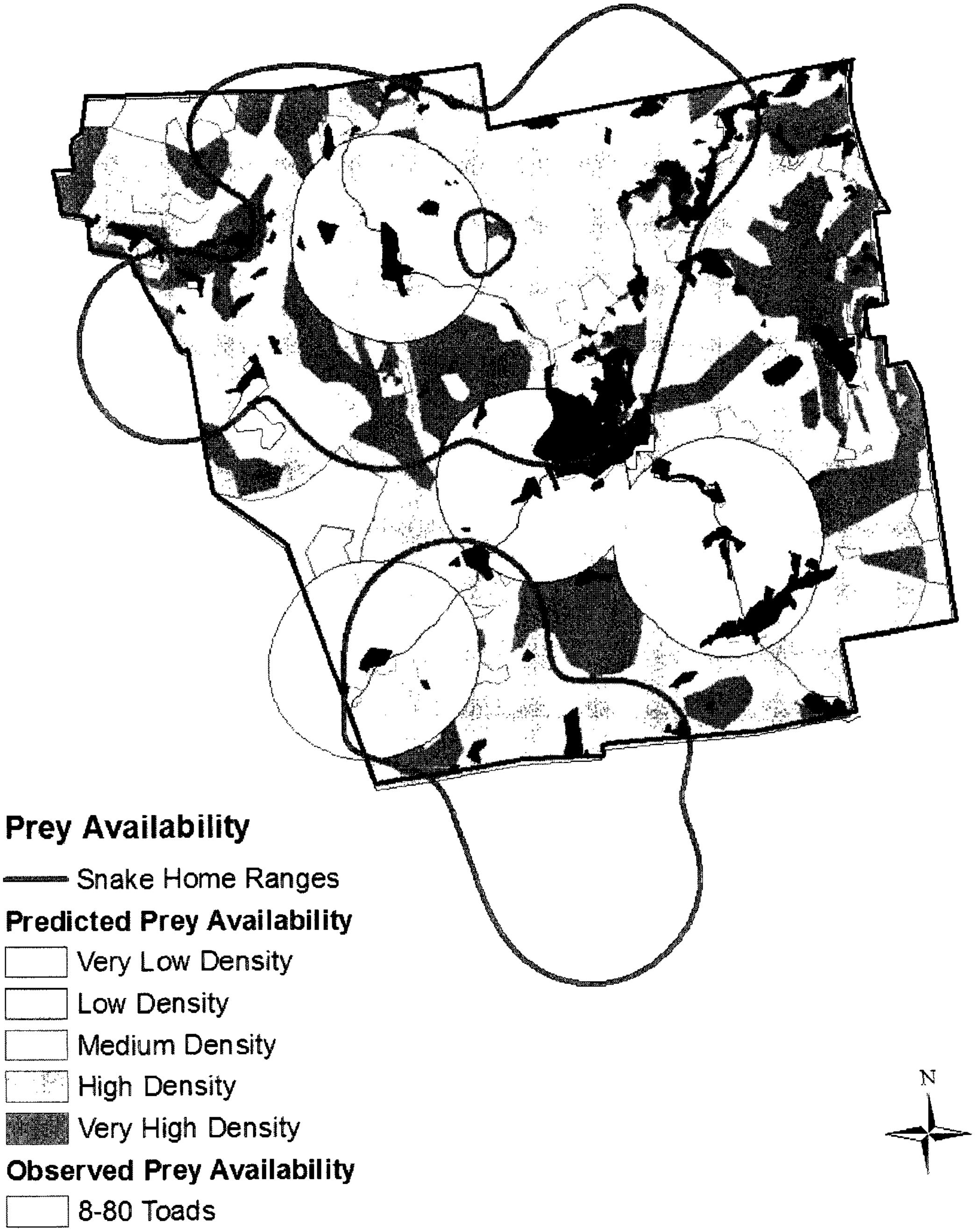

Figure B.1. Map of predicted and observed availability of prey species *B. americanus* throughout the NBAS, 2008. Predicted density indices were derived from the habitat suitability model and observed densities were derived from aural survey results.

APPENDIX C

DIFFERENTIAL PREDATION

Methods

Differential predation was examined to determine the effects of color pattern on predation frequency in the field using snake models. Potential predators occurring at the site included mammals, raptors, and crows. Models were constructed by first pressing a 90 cm hognose cast (MRR-45 WASCO, Monroe, GA) into Sculpey Model Maker (Polyform Products, Schiller Park, IL) to create a flexible mold which was then filled with Super Sculpey modeling compound (Figure C.1). The advantage of using this material is that it remains soft enough to retain beak marks of birds and tooth marks of mammals, thereby allowing for the predator to be discerned (Bittner 2003). Eighteen-gauge wire was pressed into the bottom of the model with additional wire protruding out the ventral end. Excess wire was formed into a loop and used to anchor the model to the ground. Models were painted to depict either a melanistic or patterned morph (Figure C.2). Three trials were conducted for 7 and 14 day periods from 29 July to 1 September. For each trial, a total of twenty models (10 of each treatment) were placed at 10 m intervals along On Orbit Road. To ensure independence between trials, site locations were separated by a distance of 1.5 km. At each interval, one model was positioned at the forest edge in trial 1 and 1 m from trail edge in trials 2 and 3. Equal numbers of each type of model was placed on both sides to account for variation in predation intensity between the two sides of the trail. Every two days models were checked to assess attack status. Upon observing a predation attempt, the size, shape, and position of each mark were recorded. Attacked models were then reshaped or replaced to maintain the desired sample size for each treatment. Multiple beak marks were scored as a single predation attempt and missing models were conservatively be designated as unattacked. Data were pooled across all three experimental trials. Logarithmic transformation was performed on the total proportion of attacked individuals. The Likelihood Ratio *G*-test was then conducted to determine if melansim had a measurable effect on predation frequency.

Results

Avian predation was visibly discerned by the type of marking present on the attacked model (Figures C.3 and C.4). These included either a V-shaped groove positioned laterally on the model or closely spaced, triangular-shaped stabs on the dorsal surface (Brodie 1992). Other forms of identifiable disturbances were produced from small rodents and insects, however, the models having such markings were not assigned as "attacked" as these are not natural snake predators.

A total of 4 avian attacks occurred during the duration of the study, with melanistic models receiving a greater number of attacks (3) than patterned models (1) (Table C.1). However, the difference in attack frequency between melanistic (10.0%) and patterned models (3.3%) did not differ significantly ($G = 1.12$, $P = .29$).

Discussion

Predation avoidance is a strong influential factor in both the behavior and morphology of snakes (Vences et al. 2002). Behaviorally, snakes utilize microhabitats which act to reduce their risk of detection from visually oriented predators, namely raptors. However, as ectothermic organisms, thermal conditions imposed by the environment often take precedence over safety in the selection of activity-sites. In response to such conflicting demands, morphological variability of dorsal coloration has evolved among snake populations, each of which contribute its own anti-predatory benefit (Mori and Burghardt 2001; Tanaka 2007). Among the two common color variants occurring within polymorphic populations are melanism and patterning. Melanistic individuals have the advantage of thermoregulatory efficiency which confers a protective advantage in that basking time is reduced and escape response optimized (Bittner et al. 2002; Ahnesjo and Forsman 2006). What's more, with their fast rate of heat absorption and high equilibrium body temperatures, these individuals are able to select habitat with greater canopy closure, and thus, lower predation risk (Ahnesjo and Forsman 2006). In contrast, patterned phenotypes tend be more cryptic which serves to decrease the probability of detection from avian predators through disruptive coloration. However, without the thermal advantage imparted by melanism, patterned snakes are forced to compensate for higher thermoregulatory demands by basking at greater frequencies and selecting more open sites (Ahnesjo and Forsman 2006).

The *H. platirhinos* occurring on the NBAS is one such dimorphic population, with melanistic individuals being more prevalent than their patterned counterparts. In lacking the disruptive patterning, melanistic snakes are thought to appear less cryptic to predators, and thereby, suffer higher rates of predation (Lawson and King 1996; Bittner 2003). In investigating such variation in predation frequency, plasticine models were used to determine if melanism imposed a higher vulnerability to predatory attack. Study results suggested that, in fact, avian predators did not appear to discriminate between color variants as total predatory events were statistically equal. This conclusion contradicts other previous studies which substantiated the differential predation hypothesis (Andren and Nilson 1981). Such ambiguous results may be attributed to two broad factors. First, flaws in the experimental design, i.e., timing, duration, or location, could have caused an unnaturally low frequency of predation. Study length may not have been long enough or implemented at the appropriate time to capture the true level of predatory differentiation. Secondly, model bias may have been introduced into the study. Variability in realism between the models may have skewed the predatory response, where the patterning may not have been sufficiently replicated thereby inadvertently reducing crypsis. What's more, visually oriented predators may also rely on additional cues, such as movement, in order to detect prey, therefore, without this element results may have been further affected. Alternatively, predation risk may actually be equal between phenotypes within this northern population. The costs and benefits incurred by the morphological differences in crypsis, habitat selection, and activity patterns may, on a whole, incur a similar level of risk. Hence, as demonstrated in the study, neither anti-predatory strategy would afford greater protection.

To resolve these issues, future research should consider the design elements of timing and duration. As depredation may be a naturally rare event, it could prove beneficial to run the study for a longer period of time or identify peak avian feeding periods and conduct the study accordingly. Also, examining the effect of activity-site selection on differential predation would also serve to improve study results. Because crypsis is background specific, habitat choice has a significant impact on the probability of a snake being detected. As such, by accounting for spatial variability, statistical testing would be more reliable in detecting morphological differences in predation.

Table C.1. Differential predation between melanistic and patterned *H. platirhinos* models.

Color Morph	Observed # of Attacked Individuals	Expected # of Attacked Individuals	Observed # of Attacked Individuals	Expected # of Attacked Individuals
Melanistic	3	2	27	28
Patterned	1	2	29	28

Test	Chi Square	P-value
Likelihood Ratio	1.12	.29

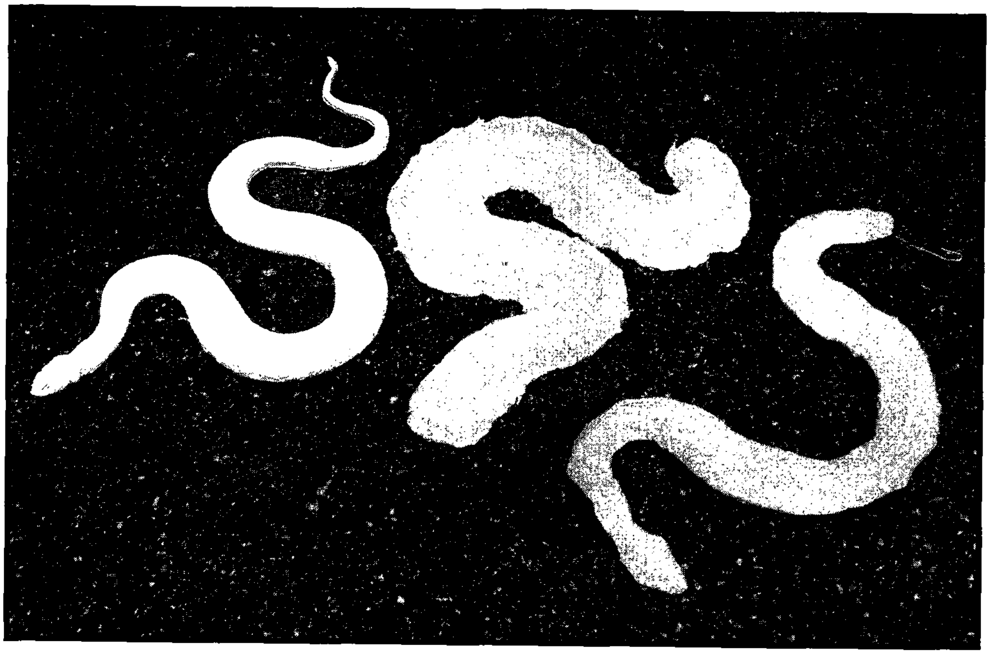

Figure C.1. Photograph of hognose replica, mold, and unpainted polymer clay model used in predation experiment in 2008.

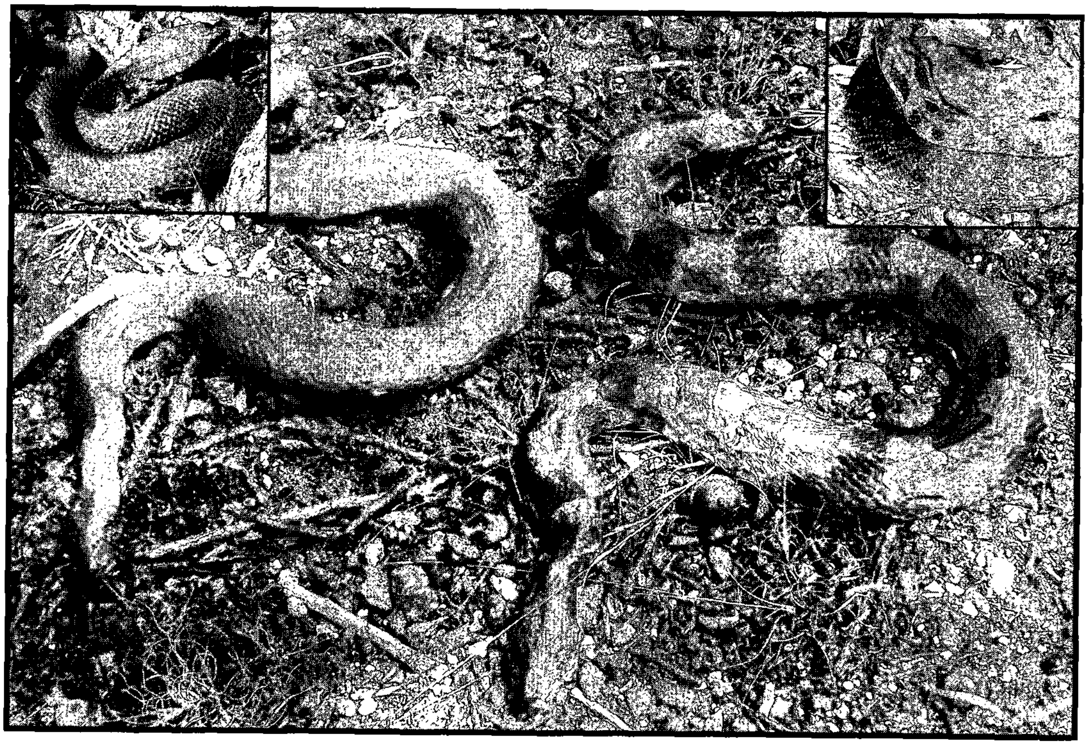

Figure C.2. Photograph of melanistic and patterned models used in predation experiment at the NBAS, 2008.

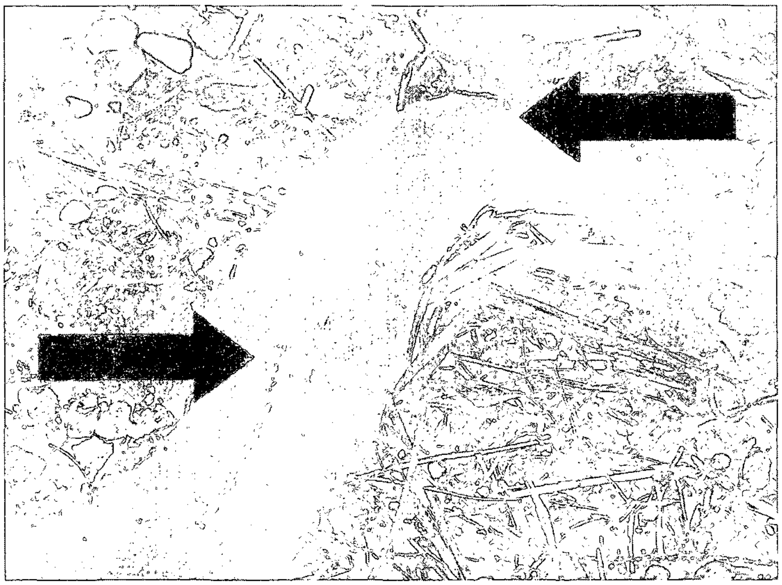

Figure C.3. Photograph of predation event on melanistic model used in differential predation experiment at the NBAS, 2008. Two sets of triangular impressions indicate avian attack resulting from talons.

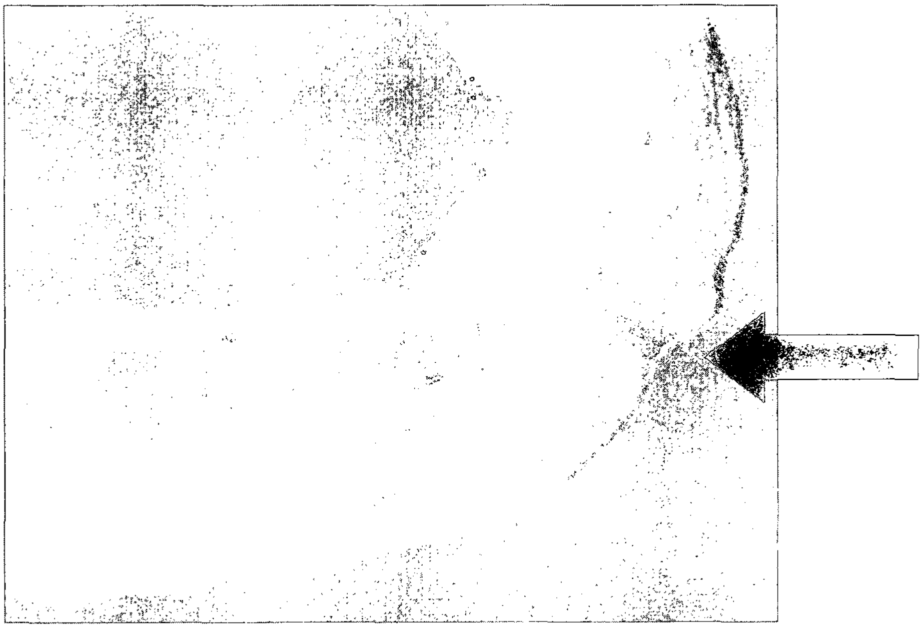

Figure C.4. Photograph of predation event of melanistic model used in differential predation experiment at the NBAS, 2008. Triangular groove is indicative of avian attack.

APPENDIX D

IACUC APPROVAL

University *of* New Hampshire

Research Conduct and Compliance Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

30-Apr-2007

Litvaitis, John
Natural Resources, James Hall
Durham, NH 03824

IACUC #: 070403
Project: A multi-scale evaluation of eastern hognose snake habitat selection
Category: D
Approval Date: 27-Apr-2007

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research involves chronic maintenance of animals with a disease/functional deficit and/or procedures potentially inducing moderate pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics.* The IACUC made the following comment(s) on this protocol:

a. In Section IV, A (experimental design), after the fourth sentence in the last paragraph, the Committee inserted "Snakes will be recaptured after 5-6 months, and transmitters removed."
b. In Section VII #3, b (implanted catheters, prostheses, etc., site), the Committee inserted "see surgical procedures."
c. In Section VII #15 (paralytic agents), the Committee changed the checkmark to "No."
d. Celine Goulet needs to complete the Medical Questionnaire prior to handling any vertebrate animals.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Roger Wells at 862-2726 or Julie Simpson at 862-2003.

For the IACUC,

Jessica Bolker

Jessica A. Bolker, Ph.D.
Chair

cc: File

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