Student Juried Paper Program – Undergraduate & Graduate

Sponsored by the Glenn and Carol Pearsall Adirondack Foundation

CHAIR: Dr. John Mills, President, Paul Smith's College

Schedule of Presentations

May 18th, 2011, 11:15 a.m., Gothics Meeting Room

Graduate:

Cathrine Haase, SUNY ESF, Moose Habitat
Courtney Lamere, SUNY ESF, Black Bear Conflicts
Abigail, Larkin, SUNY ESF, Wilderness Perceptions

John Mills, Paul Smith's College

May 18th, 2011, 1:45 p.m., Gothics Meeting Room

Undergraduate:

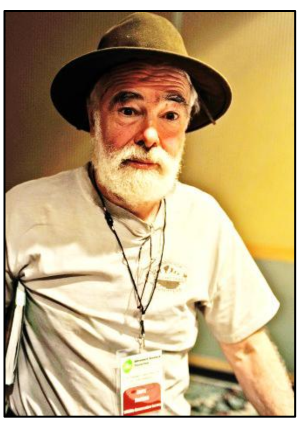
Benkamin Eck, Kim Forrest, and Alex Byrne
Paul Smith's College, Salamander Condition

Graduate:

Caitlin Snyder, SUNY ESF, Forest Floor Communities
Scott Warsen, SUNY ESF, Bird Assemblages

May 19th, 2011, 12:30 p.m., Recognition Luncheon

Jerry Jenkins, Wildlife Conservation Society



Outstanding Juried Student Paper Recognition
Chair: **Dr. John Mills**, President, Paul Smith's College
Sponsored by the Glenn and Carol Pearsall Adirondack Foundation

Presentation: 2011 Adirondack Achievement Award
Jerry Jenkins, Wildlife Conservation Society

Closing Remarks: Hon. Teresa R. Sayward
113th Assembly District

Assemblywoman Teresa Sayward

Integrating thermal cover into existing habitat suitability models for moose in the Adirondack Park of New York.

Catherine. G. Haase[1,2] and H. Brian Underwood[3]

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Moose (*Alces alces*) can survive in very cold temperatures because of their large body size, thick skin, and dense, dark coat. These characteristics make it difficult for moose to live in warmer climates, however, as they become heat stressed at temperatures as low as -5°C in the late winter months and 14°C in the summer. Chronic heat stress may lead to increased susceptibility to parasitism and disease, reduced productivity, and starvation as has been observed in the Midwestern United States, where moose populations have been significantly declining due to warmer temperatures. To combat the effects of heat stress, moose will bed in snow or immerse themselves in water to increase heat loss, stop eating to reduce metabolic heat production, or seek thermal cover to reduce the absorption of solar radiation. Therefore the interspersion of thermal shelters among habitats that offer good foraging opportunities allows moose to manage the trade-off between the acquisition of food and the dissipation of heat. To analyze the influence of thermal cover on moose habitat suitability in the Adirondack Park of New York, we integrated a thermal balance component into an existing moose Habitat Suitability Index (HSI) model.

Habitat suitability index modeling is a type of management tool that quantifies habitat quality on a scale of 0.0 (unsuitable) to 1.0 (optimal) in response to specific food and cover requirements of a species. Standardization permits comparison between habitats and can allow managers to set goals of habitat quality. We evaluated critical thermal environments for moose by using operative temperature (T_e), an index that integrates the combined effects of air temperature, total absorbed radiation, and wind speed on the thermal environment experienced by an animal. It considers the effects of pelage on heat loss and heat absorption and incorporates seasonal variation in surface albedo due to accumulated snow. By mapping T_e across the Adirondack Park, our goal was to integrate critical thermal environments for moose, in a spatially explicit manner, into an analysis of habitat suitability that can be used to evaluate the potential biotic effects of climate warming on future population distribution.

We modeled T_e spatially (Fig. 1) across the Park under three forest canopy cover-types (deciduous and coniferous and mixed) during two seasons (late winter-spring and summer). We modeled mean monthly air temperatures with respect to elevation and calculated solar radiation values transmitted through the forest canopy as a function of location, forest cover-type, and time of year. We validated these spatial and temporal patterns of T_e using heat transfer relationships in the published literature and by measuring black globe temperature (congruent to modeled operative temperatures) at random locations across the Park. Thermal cover was designated as areas where T_e values fell below the behavioral upper critical thresholds modeled from the literature.

We evaluated each habitat variable using HSI graphs from published, detailed habitat studies to designate suitability index scores. Scores were substituted into an HSI equation to evaluate each land unit and projected in ArcGIS to show habitat suitability across the park and for each season. Units with scores <0.31 consisted of low habitat suitability, those with scores >0.67 were considered highly suitable, and those in between were considered moderately suitable. We computed the percentage of the Park in each suitability class to compare our classification to a published HSI model that did not incorporate thermal cover. To validate the model, we obtained moose observations (i.e., both visual and telemetry) and projected these observations for April and July in 2 separate shapefiles onto the appropriate seasonal suitability map. We performed a X^2 goodness-of-fit test on moose locations relative to the numbers of moose expected in each suitability class based on area, and compared standardized residuals among the 3 models.

Thermal suitability was significantly lower in late winter-spring compared to summer, demonstrating to the importance of leaf phenology in modifying solar radiation transmitted through the canopy. Therefore, the separation of habitat suitability into seasonal components provides a more accurate representation of habitat quality for moose because it includes aspects of thermal biology that are important for moose survival. In the short-term, behavioral thermoregulation allows moose to survive in potentially hostile thermal environments; they trade-off time for space. Moose must be able to maintain homeostasis in the long-term, however, or face deleterious individual and population consequences. In some parts of their range, moose are suffering heat-stress complications attributable to climate warming, which emphasizes the need for a better understanding of moose thermal biology. Integrating a thermal balance component into an HSI model is critical for anticipating the effects of climate warming on habitat suitability, as the availability of thermal cover, interspersed among adequate forage, will continue to be a prime habitat consideration for moose.

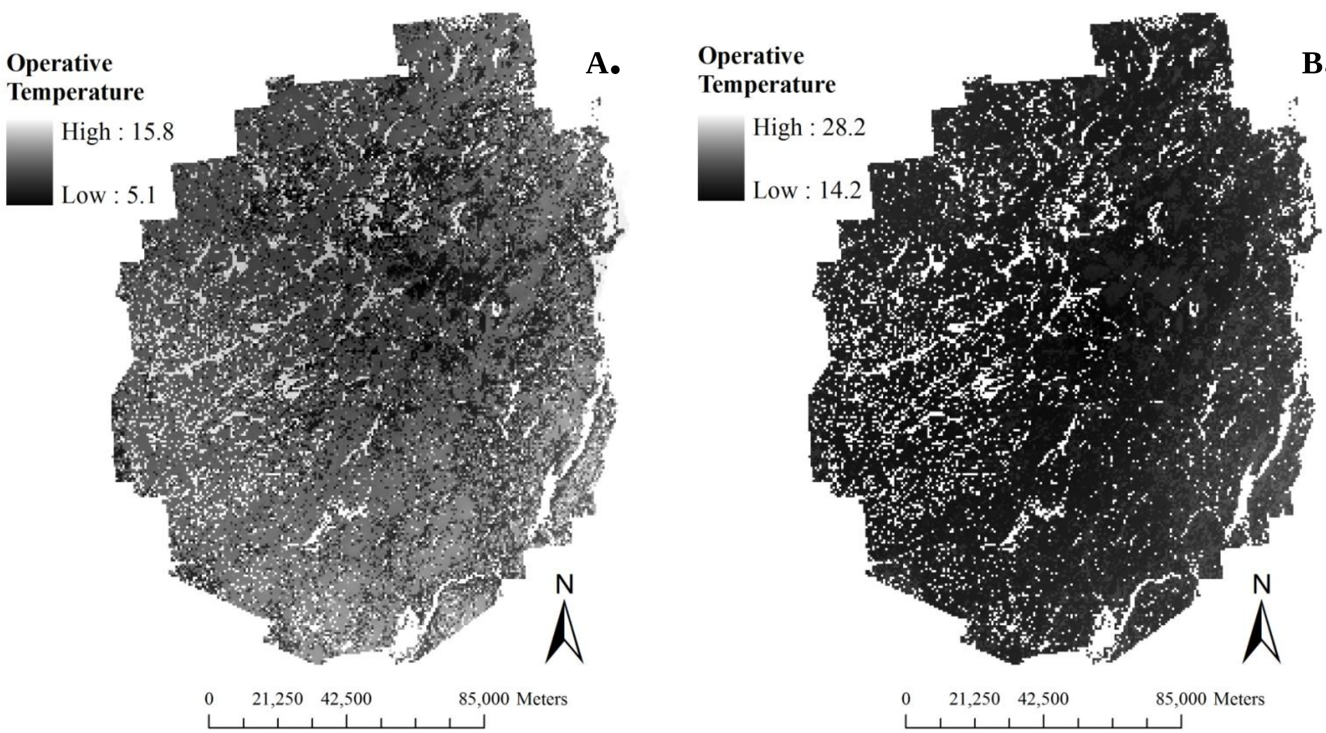

Figure 1a-b: Operative temperature (T_e) maps of the Adirondack Park in (a) April (late-winter) and (b) July (summer) months; although T_e values were lower in the late winter, the upper threshold for moose was 8C, while in summer it was 30C. This distinguishes more thermally stressful habitat in the late winter months compared to summer for moose.

Effect of Variable Mast Production on Human-Black Bear Conflicts in the Adirondack Park of New York State

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American black bears (*Ursus americanus*) in the Adirondack Mountains of New York have been an important game species and symbol of wilderness for over a century. As the bear population in the region has expanded over the last few decades, so have negative encounters with humans. While human-bear conflicts in the region are reported every summer, certain years contain significantly higher numbers of conflicts than others. Wildlife managers with the New York State Department of Environmental Conservation (DEC) suspected periodic increases in human-black bear conflicts were due to a lack of natural food, but it had not been rigorously quantified until this study.

SUNY ESF Huntington Wildlife Forest (HWF) in Newcomb, NY has shown that American beech (*Fagus grandifolia*) follows an alternate-year boom and bust cycle of mast production. American beech is the only significant hard mast species in the region producing as many as 165,000 nuts/ha in good years and 0 nuts/ha during crop failures.

The objectives of this study were to (1) assess patterns in production of natural bear foods in the Adirondacks from a 20-year dataset of forest fruit and beechnut abundance to identify periods of food abundance and food shortage, (2) quantify the relationship of natural food shortages to nuisance bear movements, and (3) develop recommendations for mitigation of human-bear conflicts based on observed patterns in food abundance and report recommendations to DEC. I hypothesized that annual increases in human-bear conflicts were positively correlated to beechnut crop failure.

HWF has recorded fruiting phenology data annually on important bear food species since 1989. Fruit abundance is ranked on a scale from 0 (no fruit) to 4 (excellent), and seed abundance is estimated using seed traps. Linear regression was used to compare nuisance complaints recorded by the DEC in the portions of Regions 5 and 6 from 2001 to 2009 that occurred inside the Adirondack Park to beechnut abundance rankings from HWF. Quantitative data on beechnut abundance (viable nuts/ha) was also compared to nuisance complaints using Pearson's correlation coefficient. Additionally, nuisance records from 1995 to 2008 from Region 5 were analyzed separately as a more complete history of bear complaints was available and the DEC suspected a 4 year cycle of peak nuisance bear activity in the region.

I identified important food species in the Adirondacks from previous research on bear food choices at HWF. With the exclusion of beech, there were 14 species of bear foods identified for which there were complete historical fruiting records (1991-2009) from the HWF Adirondack Ecological Center's Adirondack Long-Term Ecological Monitoring Program. These species included red raspberry, black cherry, apple, American mountain ash, and beaked hazelnut among others. For ease of discussion, I will refer to these other foods as soft mast.

I tested for a correlation between each of these soft mast species and nuisance black bear complaints in the Adirondack Park using the Pearson's coefficient. As black bears are opportunistic omnivores, I used the average of all the soft mast rankings per year to test correlation with the number of complaints.

Nuisance reports during the summer were negatively correlated to beechnut abundance rankings in the following autumn ($r = -0.803$). Complaints filed in the Adirondack Park are significantly higher in years with a beechnut failure than during excellent crop years ($p = 0.039$). Additionally, DEC Region 5 experiences pulses of bear complaints occurring approximately every 4 years. In this region, the mean number of human-bear conflicts is significantly higher during these peak years (1995, 1999, 2003, and 2007) than other years ($p < 0.0001$). Estimated beechnuts/ha had a significant negative correlation to nuisance complaints in Region 5 ($r = -0.711$) (Figure 1).

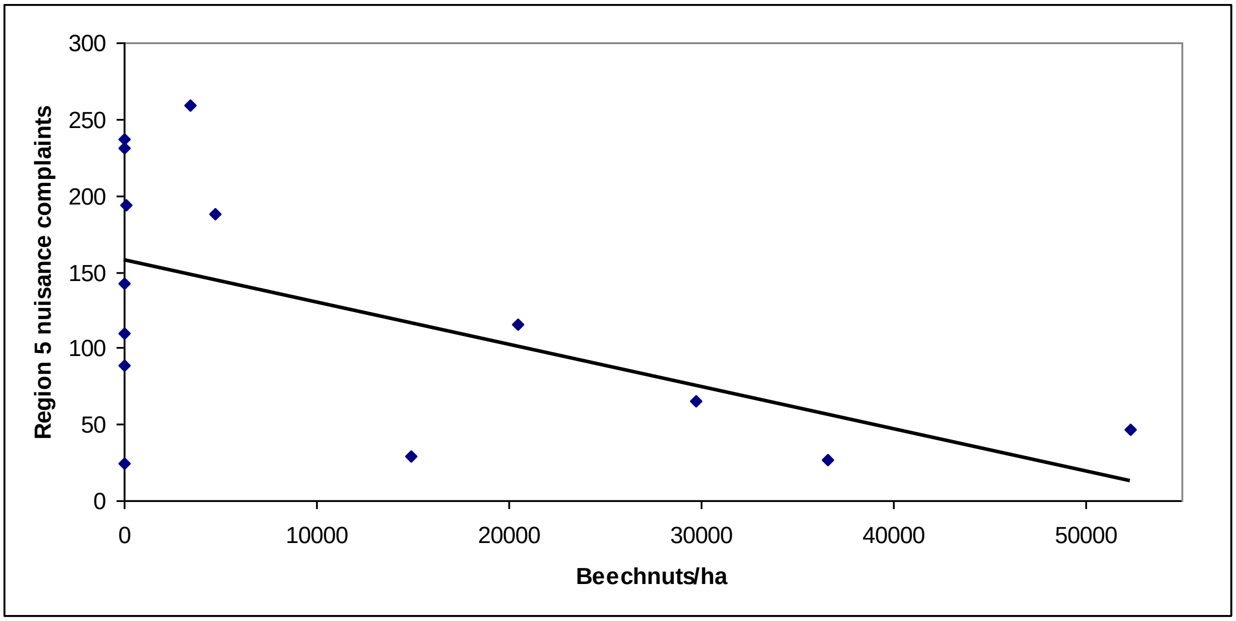

Figure 1. Black bear nuisance complaints from 1995 to 2008 in DEC Region 5 of New York State and estimated beechnuts per hectare on the SUNY-ESF Huntington Wildlife Forest.

These results lead to the question of how summer foraging and nuisance behavior is related to the failure of a subsequent fall food source. Comparison of the summer fruiting abundance ranking for soft mast species to the beechnut productivity over a 19 year period showed these species produce fruit in unison with the American beech, suggesting a common driver of masting. This finding identifies summer food sources as a possible catalyst for the increase in human-bear conflicts and as an indicator of the success of the consequent beechnut crop.

My results indicate that the DEC can anticipate summers with high levels of human-bear conflicts by monitoring the cycles of natural foods. Soft and hard mast species appear to be cycling in unison. Surveys of the foods available early in the season such as strawberry and pin cherry may predict the abundance of other summer foods and consequently the level of conflict. Tracking the beechnut crop will also help predict the behavior of bears in the summer season. Anticipating summers with low abundance of natural foods will allow the DEC to recruit volunteers and hire seasonal technicians in the years when they are most needed.

A comparative study of wilderness perceptions among Adirondack Park stakeholders based on survey results and mapping techniques.

Larkin, Abigail M.[1*] and Colin M. **Beier**[2,3].

The concept of *wilderness* that is used to designate and preserve wilderness areas is traditionally framed within a legal definition. Considering wilderness via individual and cultural perceptions provides a contrast to the traditional legal framework and challenges the way that wilderness is conventionally understood. This contrast is particularly relevant within the Adirondack State Park of northern New York, a six million acre landscape of public and private lands regulated by a system of 13 land use classifications (legal designations) that range from WILDERNESS to INDUSTRIAL USE. The Adirondack Park is the largest protected landscape of the contiguous U.S. and the only preserved area with a residential population. The unique composition of lands and stakeholders led to a complex history of conflict over land use designations that restricted local development while conserving natural resources. The protective policies developed over time disproportionately considered the interests of nonresidents over residents, typically favoring the agendas of downstate interests (nonresidents) when defining and designating areas within the range of land use classifications. Prior studies of wilderness perceptions revealed differences among stakeholder and geographic populations, and varying degrees of congruence between the extents of perceptually identified wilderness and legally defined and protected wilderness areas.

This research explored differences in wilderness perceptions among stakeholders (residents, seasonal residents, visitors) within four Adirondack communities (Old Forge, Lake Placid, Lake George, Newcomb). I surveyed the public in these four communities to determine the desirability of specific landscape characteristics (e.g. campsites) and to characterize respondents by four classes along a wilderness purism scale (nonpurist, neutralist, moderate purist, strong purist), combined with spatial information that represented each characteristic in geographic information systems (GIS) to generate wilderness perception maps for each sample population. Wilderness perception maps were constructed by aggregating layer maps created for each of the four purism classes based on a scheme that spatially represented, buffered, and excluded undesirable landscape characteristics (Figure 1).

Survey results across all geographic areas indicated significant differences in wilderness perception among stakeholder groups, with residents expressing less restrictive (nonpurist) perceptions relative to seasonal residents and visitors. The Newcomb sample had the greatest diversity among stakeholder groups with high concentrations of residents classified as nonpurists and seasonal residents and visitors (nonresidents) classified as strong purists, which reflects the continuing conflict among stakeholders over land and resource use within the Adirondack Park. Geographic and demographic (age, education, politics) factors shaped perceptions and offered potential explanations for these differences. Results based on the comparisons of wilderness perception maps indicated that seasonal residents had the largest area of perceived wilderness, despite characterization by strict wilderness perceptions (strong purists), followed by visitors and residents. Again, differences among stakeholders were particularly evident within the Newcomb sample, where residents perceived the smallest extent of wilderness relative to nonresidents. All sample group maps shared core areas of wilderness that were largely congruent with legally designated wilderness units of the

Adirondack Park. However, wilderness perception maps also identified significant areas of perceived wilderness existing outside of the legally designated wilderness boundaries. These comparisons demonstrated clear perceptual differences among sample groups and the disparity between perceived and legally designated wilderness areas in the Adirondack Park.

This research identified commonalities and important differences between perceived and legal wilderness in the Adirondacks for the consideration of managers and recreationists. The representation of survey results within a GIS demonstrated the emergent properties of the map approach, based on a complex combination of discrete spatial characteristics across a landscape that affect the extent and boundaries of perceived wilderness. Wilderness perception maps could not be predicted by survey results, which suggested that mapping is an additional tool to describe wilderness perceptions, and offers conclusions specific to the Adirondack landscape. Insights gained regarding wilderness perceptions could contribute to improved management of the landscape and a greater understanding of the diverse populations in the Adirondack Park and a sustainable balance of their needs on a shared landscape.

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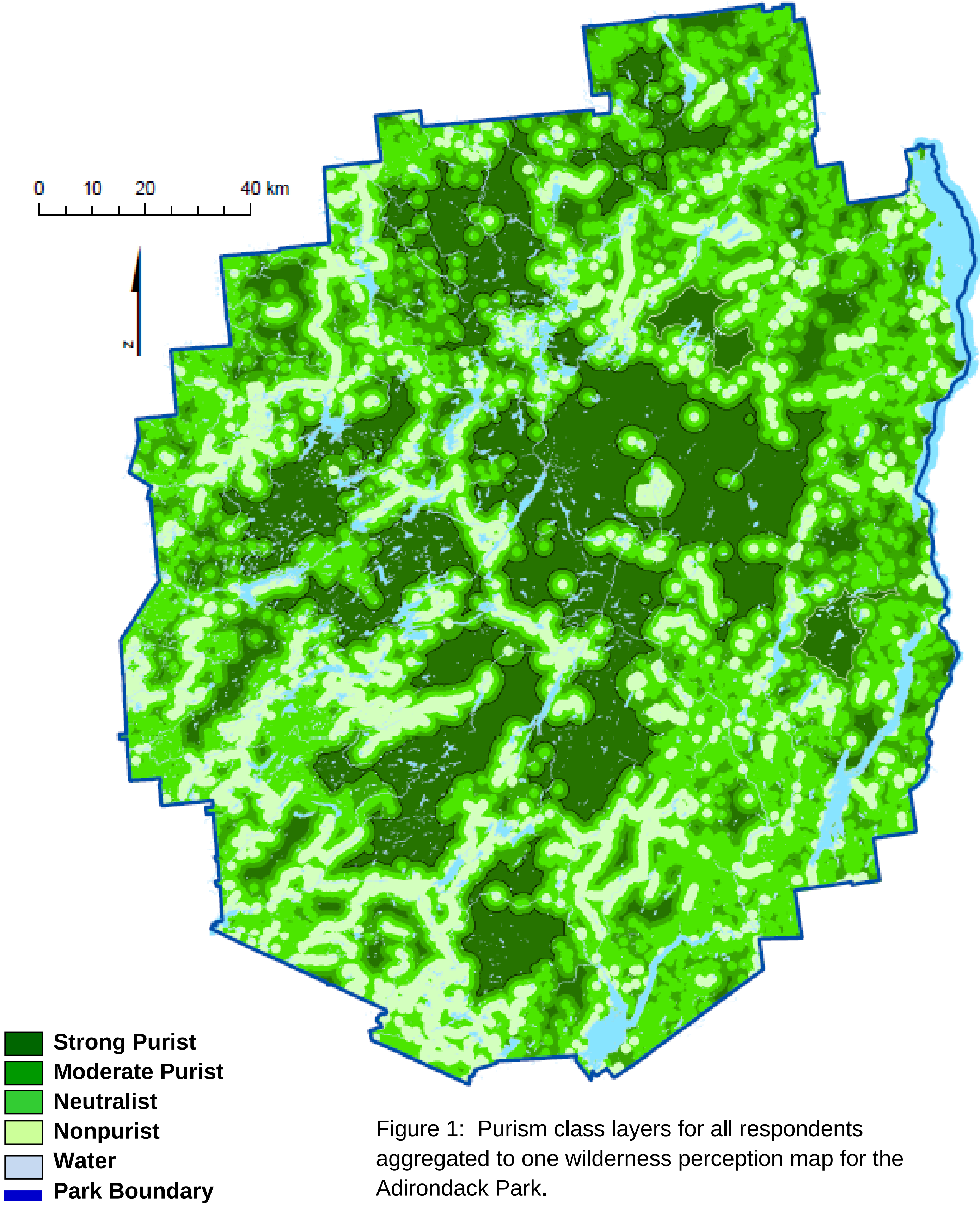

Figure 1: Purism class layers for all respondents aggregated to one wilderness perception map for the Adirondack Park.

Abundance and body condition of *Plethodon cinereus* in the Adirondack Park: a multivariate analysis of habitat use

Benjamin Eck*, Alexander Byrne*, Jenna Daub*, Ryan Deibler*, Kimberly Forrest*, Alexander LeCheminant*, Lydia Naccarato*, and Professor Celia Evans

Abstract

Much research has been conducted with respect to the influence of forest management on the widely distributed terrestrial salamander, *P. cinereus,* commonly considered an 'indicator' species due to its middle location in the food web and its sensitivity to environmental variables. However, very little is known about optimal habitat characteristics in established second growth forests as they influence the relative abundance and fitness of *P. cinereus*. We established plots (n= 49) in a mixed northern hardwood forest in the northern Adirondacks and collected a suite of habitat variables. We measured abundance and body condition of adult, juvenile and young of the year *P. cinereus* to determine the specificity of habitat use. Hanski's rule states that organisms with broad distributions will be locally abundant. One suggested hypothesis for this pattern is that species with broad distributions are habitat generalists. We hypothesized that *P. cinereus* abundance and body condition would not be strongly correlated to single habitat variables and would only be weakly described by a multivariate approach, thus suggesting they are habitat generalists. We did a Principal Components analysis to collapse all recorded environmental variables (area of coarse woody debris, litter depth, soil pH, tree species influencing plots, proportion of conifers) into six Principal component axes representing uncorrelated habitat gradients. We used these Principle Components Axes (PC axes) as the independent variables in a multiple regression approach to test against the response variables: proportion of adults, juveniles, young of the year, and body condition. Then, using a multiple regression analysis, we were able to determine how successful the PC axes (environmental variables) were in explaining the variance in response variables according to the life stage.

We found that the proportion of adults was positively correlated with mixed forest with larger trees, high component of hemlock, maple and beech, and low woody debris. Adults were negatively correlated with habitats where trees were small, and dominated by birch and balsam fir, however these PC axes only explained less than 40% of the variance in the data. Juveniles were positively correlated with habitats with small trees dominated by birch and balsam fir and

negatively correlated to habitats with a higher beech and maple component. In the case of juveniles < 25% of the variance in the model was explained. Salamanders of different life stages (adults, juveniles and young of the year) had significantly different body conditions, likely due to a combination of allometry and habitat quality. To examine the influence of habitat variables on body condition we used the residuals of the relationship between proportion of adults versus body condition, since those two were strongly correlated. Having removed the influence of adults on body condition we still found significant positive relationships between body condition and PC axes that represent habitats in which adults were relatively more abundant than juveniles. Also, adult and young of the year salamander body condition was significantly greater for salamanders found under CWD than those found in the leaf litter suggesting that microhabitat variables may be more important than plot level variables in defining quality habitat.

In working to specify what the abundance of *P. cinereus* indicates, we must consider differences in life stages and the spatial scale on which measurements are made.. Our data suggest that *P.cinereus* is a relative generalist species with regard to habitat use, however, the data also suggests that habitat partitioning occurs between different life stages.

*Authors are Paul Smith's College Students
**PhD. and Associate Professor of Ecology Paul Smiths College

"Forest floor communities in the Adirondacks across a calcium gradient: Terrestrial salamander diet, prey availability, and community composition."

Caitlin M. Snyder, Stacy A. McNulty, Melissa K. Fierke, Colin M. Beier, and Russell D. Briggs
Major Professor: Stacy A. McNulty

Over the past several decades acid deposition has shaped forest dynamics in the Adirondacks. Calcium deficiency is one consequence that may impact communities, particularly forest floor and soil organisms. Salamanders and invertebrates contribute greatly to forest processes by connecting above and below ground systems through predator-prey interactions. However, little is known about how these interactions may be influenced by calcium. Calcium-rich prey such as snails are often found in greater abundances at high calcium sites. Since there is evidence that calcium-rich prey are a necessary component of salamander diet, we hypothesized that as habitat calcium levels increased, calcium-rich prey would make up a larger proportion of salamander diet. Our objectives were to 1) characterize the prey community available to salamanders in the leaf litter 2) characterize the diet of the red-backed (*Plethodon cinereus*) and dusky (*Desmognathus* spp) salamanders, and 3) quantify the relationship between prey availability, salamander diet, and soil calcium within Adirondack hardwood forests.

The most abundant invertebrates extracted from northern hardwood litter were mites, springtails, adult flies, and snails. As soil calcium increased, the number of beetle larvae, potworms, and snails increased. Litter abundances of beetle larvae, springtails, and millipedes were positively correlated to *P. cinereus* diet abundances. In *Desmognathus* stomachs, litter and diet abundances of snails were positively correlated. However, litter and diet abundances of Oribatid mites were negatively correlated in *Desmognathus*.

A total of 1,496 prey items were identified from the stomachs of 123 *P. cinereus* and 49 *Desmognathus* across twelve sites. Oribatid mites, non-Oribatid mites, snails, and flies were most frequently eaten, while beetles, snails, various larvae, and flies contributed most to stomach content volume. The salamander species shared 67.9% of their diet. However, the two species differed in the number of springtails, Oribatid mites, non-Oribatid mites, larvae, and snails, and differed in the volume of Oribatid mites and snails. Stomach contents showed the differing importance of adult beetles, mites, and springtails in both abundance and volume. We detected few relationships between prey abundance in diet and habitat calcium. Beetle larvae percent abundance in the stomachs of *P. cinereus* was increased with calcium, while Oribatid mite percent abundance was negatively correlated. Adult beetle percent abundance was negatively correlated with calcium in the stomachs of *Desmognathus*. Percent biomass of the two species was negatively correlated. As soil calcium increased, *Desmognathus* percent biomass decreased, while *P. cinereus* percent biomass increased.

Although calcium is important in invertebrate and salamander communities, our results revealed many inconclusive relationships between litter prey, salamander diet, and soil calcium. However, our results do confirm the generalist feeding strategy common to woodland salamanders. Red-backed and dusky salamanders differ in their consumption of some important prey groups, but overall the two most abundant species have a very similar and diverse diet. Particularly, calcium-rich snails and mites are important to red-backed salamanders. It is possible that salamanders exploit a wide range of microhabitats and diversity of prey because of the cool and moist Adirondack climate which offers optimal foraging conditions. *P. cinereus* ate a greater number and volume of Oribatid mites and snails, both calcium-rich prey, than *Desmognathus*. Other diet studies found *P. cinereus* consumed a large quantity of calcium-rich prey and contained a relatively high calcium content. This could help explain why we found many *P. cinereus* and few or no *Desmognathus* at higher calcium sites, while the opposite was found at lower calcium sites. However, the lack of relationships between available prey, calcium-rich prey consumed and habitat calcium may verify that salamanders do not specialize on particular prey taxa, even in acidified areas where calcium appears to be limited.

Indirect effects of acid deposition on calcium depletion, although lessened over the past couple of decades, may have important implications on salamander prey, feeding strategies, and forest floor food web interactions. By studying calcium through multiple trophic levels, we can better assess impacts of acid deposition on the biodiversity and integrity of our northern forests.

Patterns in Bird Assemblages across Islands in an Adirondack Lake

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INTRODUCTION

A common pattern in fragmented landscapes such archipelagos and habitat patches is the nestedness of biotas. Nestedness occurs when the assemblage of species on islands with fewer species comprises an ordered subset of the species on subsequently richer islands[1]. The chain of islands within New York’s Cranberry Lake makes it an ideal location to test established rules and patterns in biogeography and community ecology.

METHODS

Study Area

Located in the western foothills of the Adirondack Park, Cranberry Lake was dammed and inundated in 1865, raising the water level by more than 5m and doubling its surface area to the current size of 2823 ha[2]. As a result, there are over 30 islands within the lake, ranging in size from <0.1 ha to 42 ha, and dominated by a mixed hardwood-conifer forest.

Sampling Methods

Bird surveys were conducted on 27 islands during May and June 2010 using line-transect surveys conducted from 30 minutes after dawn until 10:30 AM[3]. Parallel transects spaced 75m apart were walked at a relatively constant pace (approximately 2 km/hr) by a trained observer, and all birds seen or heard were recorded. The goal was to exhaustively survey each island, so double-counting individuals was not a concern[4]. A minimum of 20 minutes was spent on each survey, and islands were surveyed on at least three separate occasions, with additional surveys conducted until a confident species list was compiled.

To examine the relationship between vegetation and species richness[5], both vertical density of vegetation and canopy cover were recorded at a series of random points on each island. Vertical density of vegetation was measured using a vertical cover board[6], and canopy cover was measured using a vertical sighting tube[7].

Statistical Analyses

The extent of nestedness was quantified by the matrix temperature[8], T, of the binary presence-absence matrix using program BITMATNEST[9]. To determine the factor(s) likely driving patterns of nestedness in this system, Spearman rank correlations were performed between the nestedness ranking of sites produced by BINMATNEST and the ranking of sites with regard to four independent variables thought to be driving species richness: area, isolation, vegetation density, and canopy cover[10,11].

Species richness was modeled as a function of the four habitat variables used in the determination of nestedness, with 11 candidate models chosen a priori, based on knowledge of this system[12]. Variables were natural log transformed to normalize residuals, and linear regressions were performed. Models were evaluated based on Akaike's Information Criterion[13] (AIC) and model weight (w_i). To rule out possible multicollinearity effects, correlation among predictor variables was calculated using Pearson's R^2.

RESULTS

A total of 36 bird species were detected throughout the study area, with individual site richness ranging from one to 18 species. The matrix temperature, *T*, of the presence-absence matrix was 4.95, which is significantly lower than the mean *T* value of 1000 random monte-carlo derived matrices generated by BINMATNEST ($\overline{T}$ = 47.18; SE = 1.33; $p < 0.01$). Spearman partial rank correlations indicate that the nested distribution is significantly correlated with the ranking of sites based on area (ρ=0.85; p<.0.01) and vegetation density (ρ=0.42; p=0.04). Of the eleven candidate models for predicting species richness on islands, the two most likely models, based on evaluation of AIC and Akaike weight, w_i, were:

(1) Ln Richness = 2.01 + 0.47 (Ln Area) + 0.49 (Ln Vegetation density), and

(2) Ln Richness = 2.06 + 0.46 (Ln Area) + 0.50 (Ln Vegetation density) + 0.16 (Ln Canopy cover),

with both models having an equal Akaike model weight (w_i = 0.21) and AIC value (Figure 1). The test for multicollinearity revealed no pair of predictor variables had a correlation higher than R^2 = 0.04.

DISCUSSION

The significantly low value of the nestedness matrix temperature for this system ($T = 4.95$) indicates a highly ordered structure to the species assemblages across islands sites with relatively few unexpected presences or absences. Possible T values for this metric range from 0 for a perfectly ordered system to 100 for a system absent of all order. While nestedness in larger-scale systems is often driven by selective colonization and extinction[14], in this system it is correlated most strongly with area and vegetation density. Given the equality of models (1) and (2) for predicting species richness, the principle of parsimony leads us to select model (1) as the best model, as it uses the smallest number of parameters while still adequately representing the data.

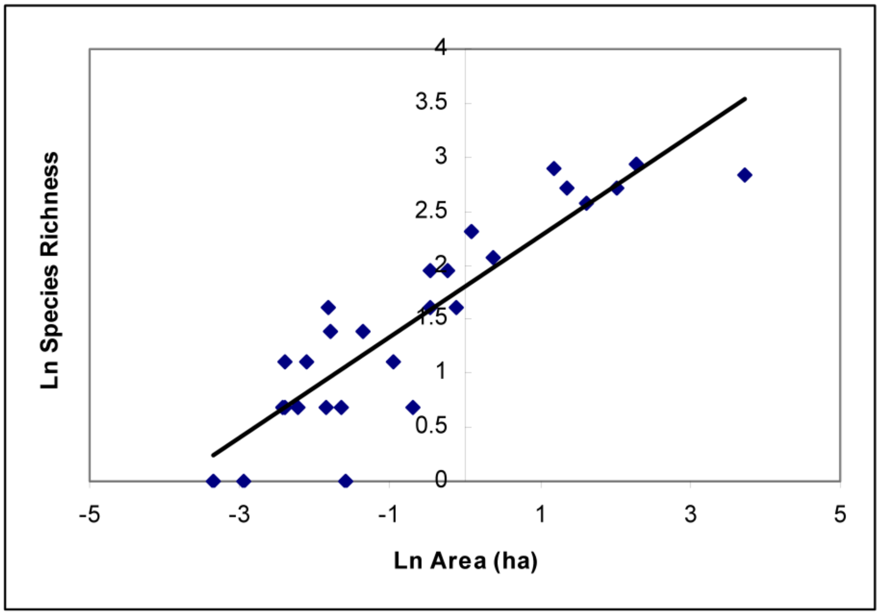

Figure 1. Comparison of observed data to predicted values for Model (1) when vegetation density is held at its mean and area is allowed to vary.

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