Moose Herbivory: a Keystone Ecological Process in the Northern Forest Influencing Biodiversity

Principal Investigator: Allan Strong
Affiliation: Rubenstein School of Env & Nat Res
Email: allan.strong@uvm.edu
Mailing address: 220L Aiken Center
University of Vermont
81 Carrigan Drive
Burlington, VT 05405

Co-Prin. Investigator: Lynn Christenson
Affiliation: Vassar College
Email: lychristenson@vassar.edu

Collaborators & Affiliations:
Nicholas Rodenhouse, Wellesley College
T. Scott Sillett, Smithsonian Migratory Bird Center

Completion date: 30 June, 2012

Moose significantly change the structure and function of the understory in the Northern Forest. Their influence extends beyond plants to include indirect effects on nest selection of sympatric migratory birds.

Funding support for this project was provided by the Northeastern States Research Cooperative (NSRC), a partnership of Northern Forest states (New Hampshire, Vermont, Maine, and New York), in coordination with the USDA Forest Service.
http://www.nsrcforest.org

Project Summary

Ecological processes are critical for maintaining biodiversity. Anthropogenic stress on ecological communities increases their vulnerability to extirpations and extinctions of species and with them go also the networks of relationships. These interactions may play critical roles in shaping life history strategies. In the Northern Forest, herbivory by large ungulates is a keystone ecological process with direct and indirect effects on other trophic levels. Over much of their range, browsing by moose (*Alces alces*) has been shown to induce changes in plant morphology, reduce tree growth and survival, and shift competitive balances. In the Northern Forest, some plants double as winter moose browse and spring/summer bird nesting substrate. By browsing only plants exposed above snowpack, moose alter nesting habitat and reshape the architecture of the understory. Here, moose and black-throated blue warbler (*Setophaga caerulescens*) engage in a cross-trophic relationship through their utilization of plants in the forest understory, particularly hobblebush (*Viburnum alnifolium*).

This research added to an existing long-term survey of bird abundance and distribution. We tested the hypothesis that the effect of moose herbivory leads to changes in the distribution and branching patterns of understory shrubs, leading to changes in habitat selection for black-throated blue warbler. Using an established sampling grid, we measured moose activity, understory composition and structure, and bird abundance. We modeled the effects of moose activity on understory plant morphology and tested for correlations in distribution of species. We also compared characteristics of hobblebush patches surrounding black-throated blue warbler nest sites with randomly selected adjacent patches.

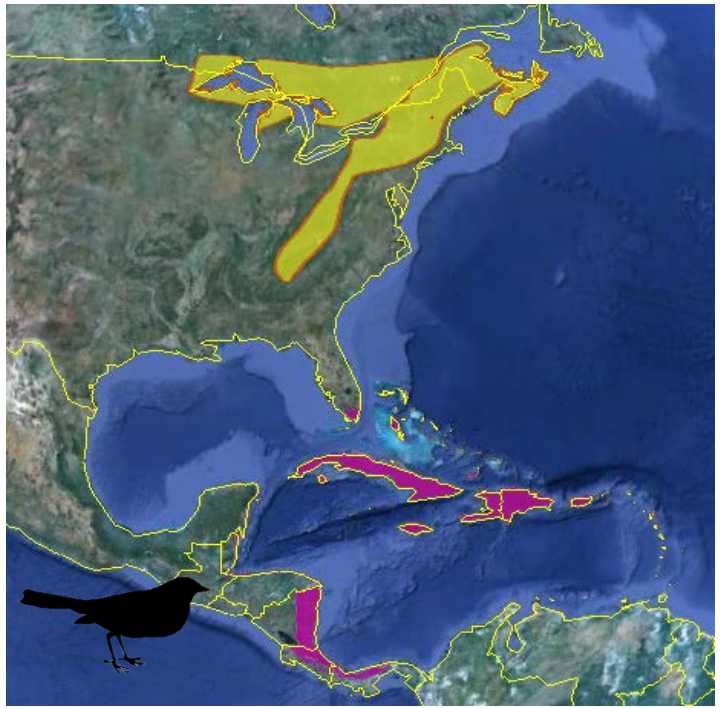
In the Northern Forest community, moose, hobblebush and black-throated blue warbler engage in a multi-trophic relationship. This study yields new information about each species, their ecological community relationship, and the study of habitat use. Our results show that 1) moose, through the act of winter browsing on buds and twigs, have a profound physical effect on hobblebush and 2) black-throated blue warbler select nest sites based on physical attributes influenced by moose herbivory. A moose browses a patch of hobblebush and the plants develop more branches than they would otherwise. Browsed plants create more structurally complex microhabitats (also measured in terms of visual obscurity). Within their own territories, black-throated blue warblers prefer patches with more branches (moose browse effect) and greater visual obscurity for nesting. Moose returned to the Northern Forest ~30 years ago but this relationship likely preceded their extirpation. Since recolonizing, moose have become a charismatic species symbolic of the Northern Forest. Moose populations contribute to wildlife watching and ecotourism in the region. While these two species' ranges overlap, under forces of global change, they may not always, and understanding the community dynamics and habitat preferences of species may be critical for long-term management as habitats and communities reorganize.

Background

- Complex ecological community relationships are often poorly understood
- These relationships may critically support threatened or rare species
- Ungulate herbivory is a key ecological process in many ecosystems
- Composition and structure of understory vegetation is a key component of habitat quality for many songbirds in the Northern Forest.

Background

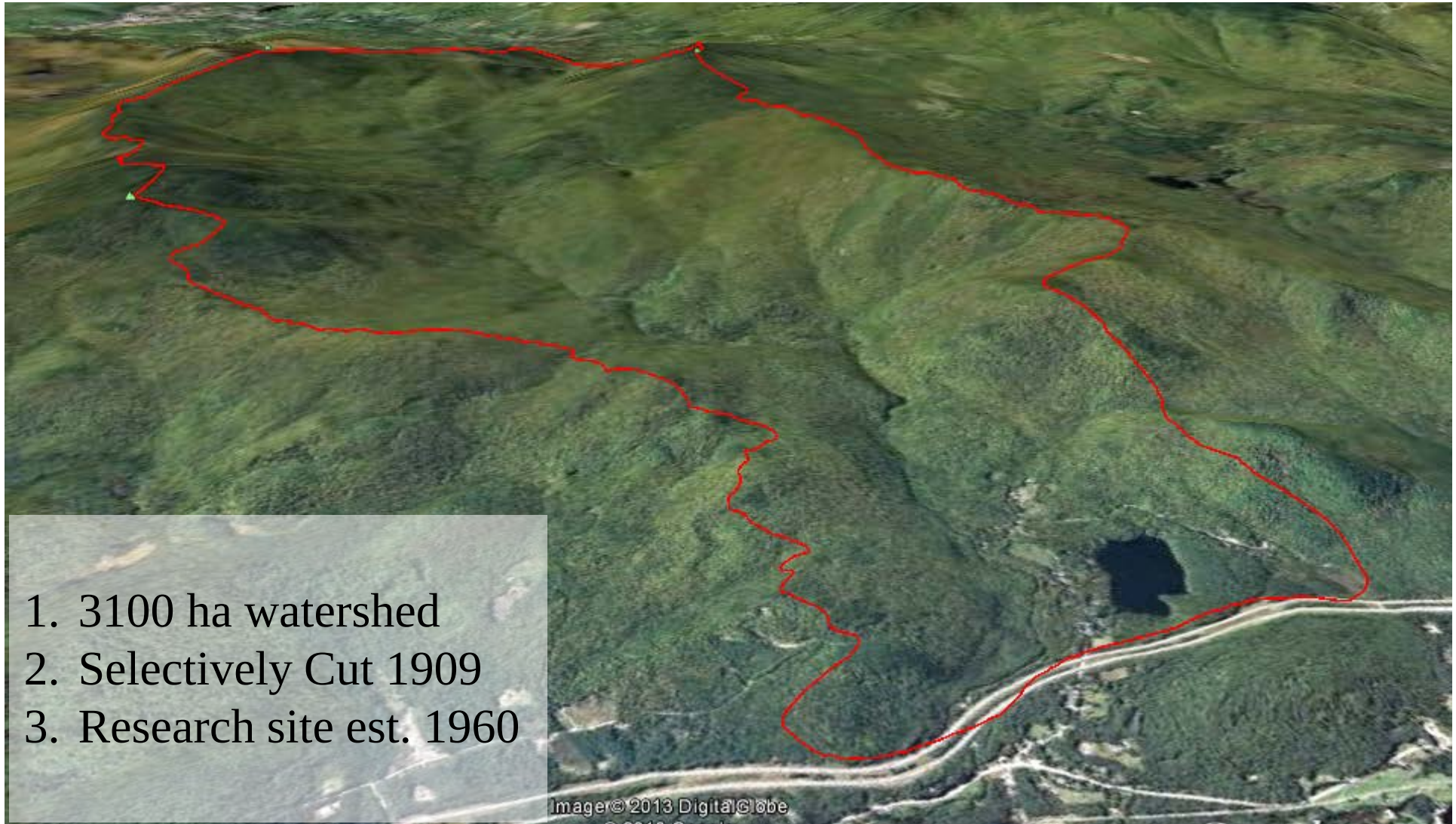
- Moose densities have fluctuated dramatically over the course of the last 200 years
- Global change will likely alter many of the components that affect or are affected by moose and may have a synergistic affect with changing moose populations



Methods: Field Sampling

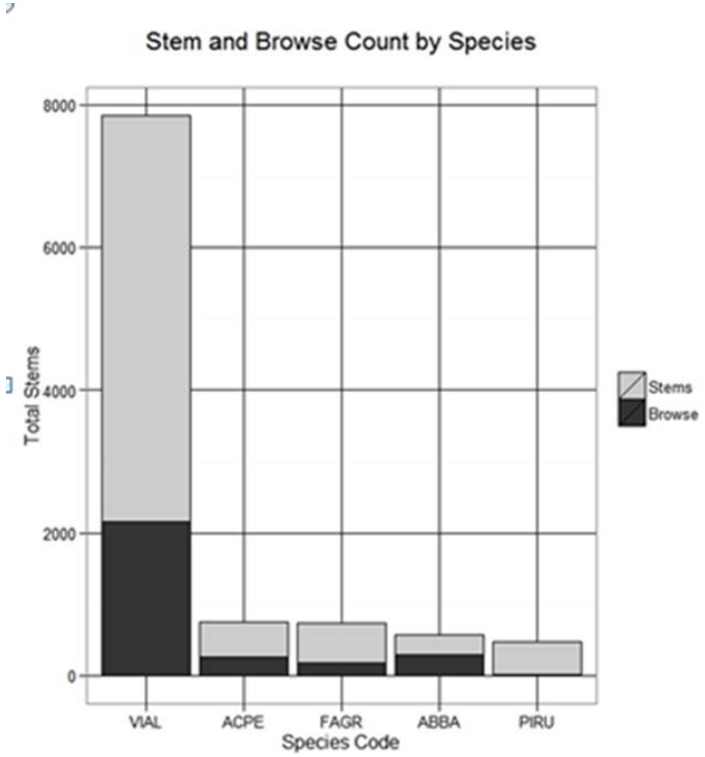
- **Extent and severity of moose browse within the Hubbard Brook Valley**
  - Surveys conducted in 2009 across Hubbard Brook
    - Abundance, distribution and morphology of understory vegetation
    - 15 north-south transects separated by 500 m
    - 298 50 m radius plots
    - Sampling at eight regularly spaced 1 m^2 subplots.
  - All woody plants in each subplot recorded by species and height category (0.3-1 m, 1-2 m and 2-3 m).
    - Presence or absence of browse was noted for each plant.
    - In 2010, one hobblebush plant in each of the 298 plots was selected at random to assess effects of browse on hobblebush structure; we recorded height of tallest bud, counts of branches and leaves, and number of branches with browse
- **Extent and severity of moose browse around Black-throated Blue Warbler nests**
  - 1m radius plots were established centered on nests constructed in hobblebush, paired with a 1m radius non-nest hobblebush patch selected at random.
    - Non-nest sites remained inside the BTBW territory and were selected for apparent similarity in the stem density and size of the hobblebush patch.
    - For each nest/non-nest plot pair, all hobblebush stems were counted and measured for height of tallest bud, number of leaves, number of branches and number of browse occurrences.
    - Within each plot, hobblebush stems less than 30 cm in height were counted but not recorded for other morphological characters.
    - Percent visual obscurity estimates were recorded in the 4 cardinal directions at distances of 5 and 10 m from the nest using a 2.5 m pole stratified in 0.5 m increments.

Methods: Study Site
Hubbard Brook Experimental Forest, NH



Methods: Study Species

Results: What are the effects of moose on hobblebush?



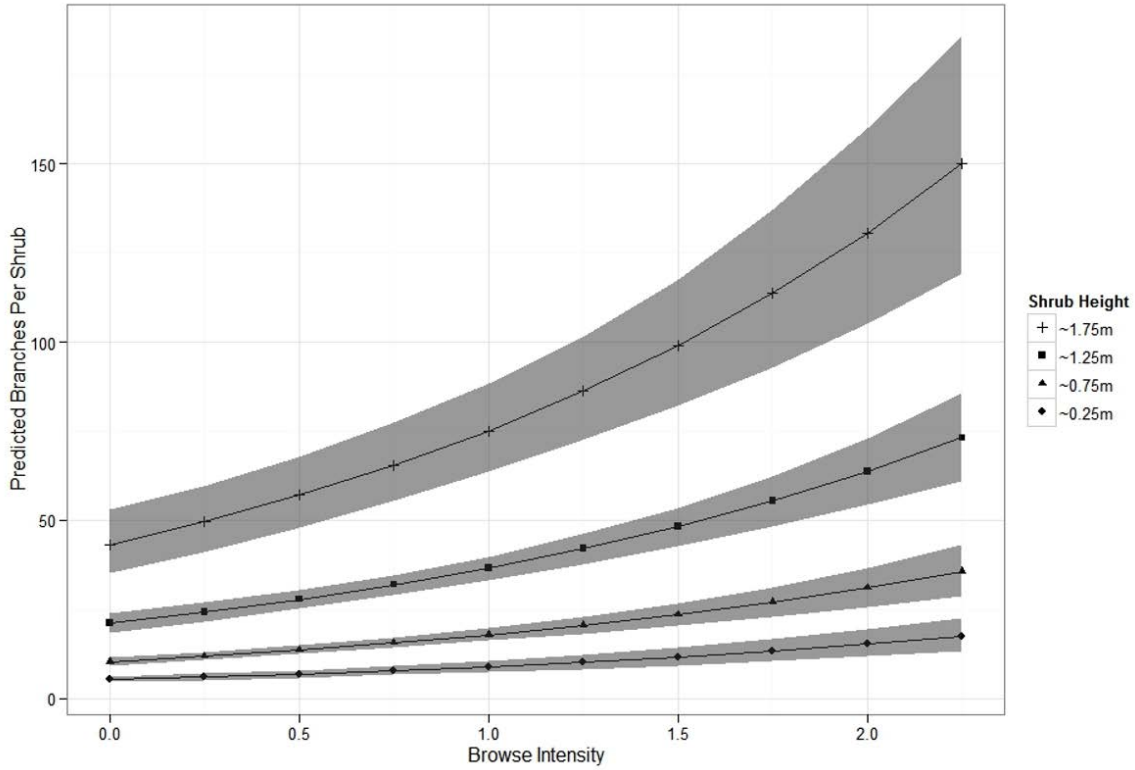
Hobblebush is the most abundant understory woody plant species and the most frequently browsed

Results: What are the effects of moose on hobblebush?

Model	AIC	Δ AIC	SBC	Δ SBC	Pr (>|t|)	Estimate
Intercept	2282.704	Null	2289.916	Null	2.03E-160	3.21E+00
Height	2125.063	157.641	2135.88	154.036	1.07E-34	1.609
Browse	2214.364	68.340	2225.181	64.735	1.62E-16	0.7248
Shrub Dens	2267.171	15.533	2277.988	11.928	5.15E-05	0.4063
Elevation	2275.71	6.994	2286.527	3.389	2.65E-03	0.7473
Northing	2279.817	2.887	2290.634	0.718	0.03	-0.2019
Diff. Light	2284.541	1.837	2295.358	5.442	0.69	0.04912
TWI plus	2283.456	0.752	2294.274	4.358	0.26	0.4896
Slope	2281.989	0.715	2292.806	2.89	0.10	0.2641
Easting	2283.083	0.379	2293.9	3.984	0.20	0.141

Hobblebush morphology (number of branches per plant) was significantly affected by plant height and moose browse intensity.

Results: What are the effects of moose on hobblebush?



Bootstrap results to predict branches per hobblebush shrub from hobblebush morphology survey at HBEF during 2010. The number of branches per plant increases with moose browse but the effect size is relative to the plant height.

Results: What factors influence nest-site selection in BTBW?

Summary of key plant and patch morphological measures for hobblebush measured at HBEF in Grafton Co, NH in 2011. Where differences are statistically significant, change ratios are expressed in terms of percent greater at nest site patches than non-nest site patches.

Varaible	Measure	Hypothesis supported?	*p*	Change Ratio (%)
Plant Density/Plot	Count	No	0.1069	
Branch Density/Plot	Count	Yes	0.0041	**40.1**
Plant Height (cm)	mean/plot	No	0.6625	
Plant Branch Count	mean/plot	Yes	0.0055	**25.7**
Plant Leaf Count	mean/plot	Yes	0.0083	**16.7**
Plant Browse Count	mean/plot	Yes	0.0234	**57.5**
Visual Obscurity/Plot	mean percent	Yes	0.0000	**9.2**

Results: Summary

- Moose browsing stimulates “shrubbier” growth form in hobblebush with greater leaves per shrub
- Patches of hobblebush that support BTBW nests show greater moose browse, greater number of branches and leaves per plant, and greater visual obscurity

Project Outcomes: Outreach

- Worked with Hubbard Brook Research Foundation (HBRF) to train and include 4 New Hampshire high school science teachers in field research team

- Partnered with HBRF and teacher Sarah Thorne to create a curriculum based on moose browsing ecology for high school science classes.

Project Outcomes: Outreach

- "Moose Power" curriculum plan includes field data from this study and is available for science teachers to download from the HBRF website.

- Sarah Thorne and Jackie Wilson presented "Moose Power" at a training that fulfilled New Hampshire science teacher continuing education unit requirements.

Hubbard Brook Environmental Literacy Program
Data Inquiry Activities

Moose Power	
Summary	Four part lesson in which students 1) investigate moose nutrition and energy requirements, 2) mimic moose browsing behavior in the forest, 3) examine data to investigate the impact of browsing on shrub structure, and 4) examine impact of shrub structure on bird nest siting.
Subject areas	Biology, Environmental Science
Skill level	Advanced
Objectives	Students will be able to: • Describe the nutritional needs and digestive adaptations of moose. • Identify how factors such as disturbance, forest succession, and climate change can affect moose. • Develop field research skills and techniques. • Interpret data gathered from field research as well as from Hubbard Brook Experimental Forest to draw conclusions about effect of moose browse upon ecosystem, specifically bird nesting habitat.
NH Science Framework Standards	• SPS1:11:2.2 Represent and understand results of investigations. • S:LS2:11:1.3 Identify the factors in an ecosystem that can affect its carrying capacity. • S:LS2:11:1.4 Analyze and describe how environmental disturbances, such as climate changes, natural events, human activity and the introduction of invasive species, can affect the flow of energy or matter in an ecosystem.
Time	Five 45-50 minute periods

Implications and applications in the Northern Forest region

- The interruption of apical dominance by moose browsing activity enhances those morphological characteristics selected for by BTBW and results in a complex, multi-trophic relationship such that moose herbivory increases habitat quality for an understory songbird.
- Preferential selection of nest sites in areas of higher density vegetation intuitively seems related to concealment from predators.
- An argument for moose as keystone modifiers in this relationship is problematic as the absence of a keystone modifier should lead to the disappearance or decrease in abundance of the species dependent on their “modifications.” At Hubbard Brook, BTBW were present in similar abundances prior to moose recolonization. Thus, moose may be better described as ecosystem engineers for their role in modifying understory vegetation structure.

Implications and applications in the Northern Forest region

- Moose make foraging decisions to maximize efficiency, focusing their energy on patches with a greater density of food resources. This spatial variation in foraging effort by moose increases understory heterogeneity across the landscape.
- Moose browse hobblebush in winter months. The buds and twigs available are dictated by the depth of snowpack. BTBW are among the first migrants to return in spring and their return coincides with the early leaf-out of the frost tolerant hobblebush. BTBW nests are most often found at heights just below the depth of peak snowpack (72-106 cm).
- Although it is difficult to predict year-to-year variations in climatic conditions, we predict that this relationship will change with decreasing snowpack as increasing temperatures prevail in the northern forest region.
- Numerous studies have shown severe negative effects of cervid browse on understory plants and bird populations but few if any positive relationships have been described between large mammalian herbivores.

Future Directions/Questions

- Can these results be duplicated in a more controlled environment?
  - By constructing moose exclosures hobblebush development and morphology could be studied in a systematically and side-by-side
  - A greenhouse study with artificial “browsing” could further substantiate how moose impact understory architecture and answer questions about other physical and chemical plant responses
  - Moose exclosures could also yield new information about proximal habitat cues for BTBW by removing moose and moose browsed plants as stimuli

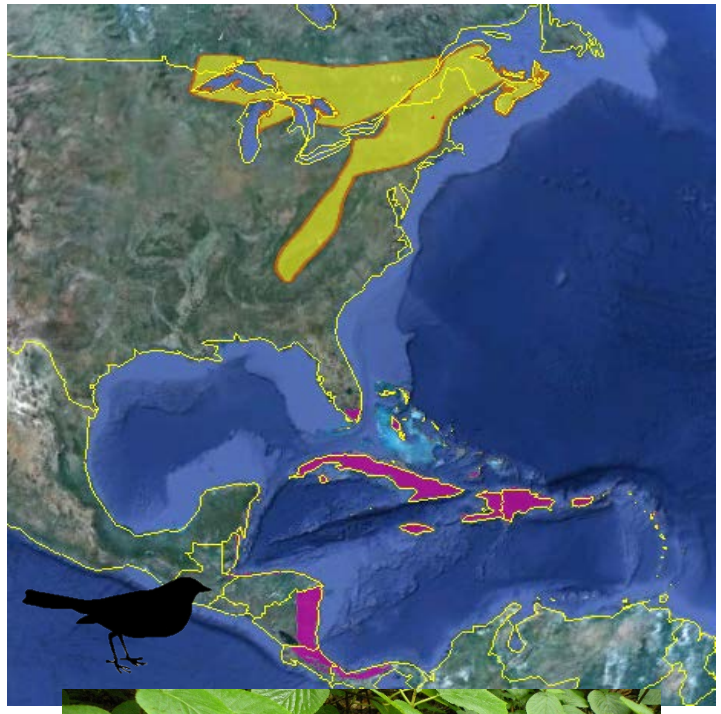
Above: Moose exclosure in Kenai Peninsula, MI (peninsulaclarion.com)

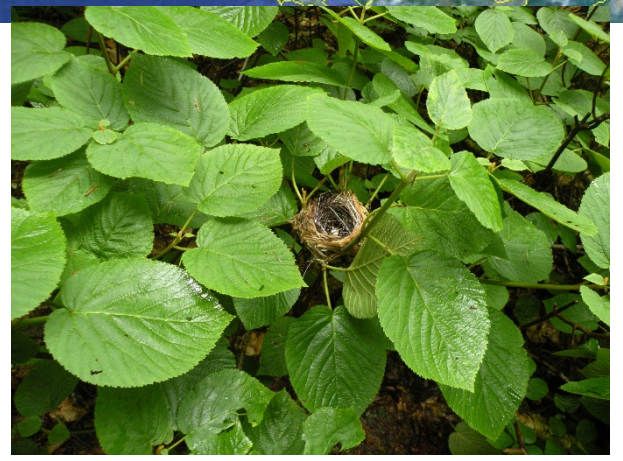
Left: Harvard Forest Invasive Plant Greenhouse study (harvardforest.fas.harvard.edu)

Future Directions/Questions

- How are proximal habitat selection cues different across the range of BTBW?
  - Using habitat cues and measurements from this study, repeat habitat measurements and paired comparisons in other areas where BTBW nest.

- Are BTBW cuing in on visual density or nest stability?
  - In other parts of BTBW range hobblebush is not as prevalent. When selecting other plants as substrate are they chosen based on how well nests are hidden or how well nests are supported?





List of products

Peer-reviewed publications

(in preparation)

Strong, A.M., T.S. Sillett, L. M. Christenson, N.L. Rodenhouse and M.J. McDonald. Moose Browse Influences Nest-site Selection of an Understory Songbird.

Other publications

"Moose Power." By Sarah Thorne and Jackie Wilson. Part of the Hubbard Brook Environmental Literacy Program Data Inquiry Activities. hubbardbrookfoundation.org

Seminars

Princeton-UVM Research Exchange *"Indirect Effects of Moose Browse on Nest-site Selection in Black-throated Blue Warbler"* March, 2014. Burlington, VT

Hubbard Brook Ecosystem Study 49th Annual Cooperators' Meeting *"Multi-trophic Interactions: Moose and Black-throated Blue Warbler at The Hubbard Brook Ecosystem Study"* July, 2012. West Thornton, NH

Northeast States Research Cooperative Research in Progress Seminar Series "*Are Moose Ecosystem Engineers?"* Nov, 2011. Burlington, VT

Hubbard Brook Ecosystem Study 48th Annual Cooperators' Meeting. *"Moose and Black-throated Blue Warblers: Commensalism?" July, 2011. West Thornton, NH*