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Trophic Cascade Effects of Deer Overabundance on Connecticut's Native Vegetation and Small Mammal Populations

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Trophic Cascade Effects of Deer Overabundance on Connecticut's Native Vegetation and Small
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TROPHIC CASCADE THEORY

Ecological communities can be regarded as a linear arrangement of interacting links in a chain. Most notably, it is found in the interacting links of primary producer, primary consumer, and secondary consumer (Fretwell 1987). When one link is destabilized, that destabilization cascades through all other connected links in the chain. Furthermore, the interacting links can be seen as a series of direct and indirect interactions. Direct actions can be seen as predation, herbivory, mutualism, commensalism, parasitism, competition, amensalism, and neutralism (Moon et al. 2010). Direct effects can be quantified as the positive or negative impact of one individual on another without the mediation of a third party. Conversely, indirect interactions are defined as the impact of one organism or species on another mediated by a third. Wootton (1993; 1994) further described this interaction as species A (donor) having an effect on species B (transmitter), which then affects species C (recipient). This interaction can be accomplished by the donor altering the abundance of the transmitter thereby affecting the recipient species. Another method occurs when the donor alters some attribute of the transmitter, such as behavior, thereby affecting the recipient (Moon et al. 2010). Indirect interactions must consist of at least two direct effect interactions. Menge (1995; 1997) identified several models of indirect interactions, one of which is a trophic cascade (Schmitz et al. 2004; Terborgh and Estes 2012).

A trophic cascade is the culmination of both direct and indirect interactions, seen in Figure 1. The direct interactions consist of two forms of predation. The first form is between predator and herbivore, causing a reduction in herbivore abundance. The second form of

predation occurring is between herbivore and basal species, or vegetation, also seen in the reduction of the basal species through consumption by herbivores. However, when all three trophic levels are involved with their corresponding direct interactions, it results in an increase in basal species as herbivores are reduced by predators. The culmination of these three interacting parts results in the aforementioned trophic cascade, most often seen as the downward effects of predators on correlated trophic levels.

Predators

P

-

Herbivores

P

-

+

Vegetation
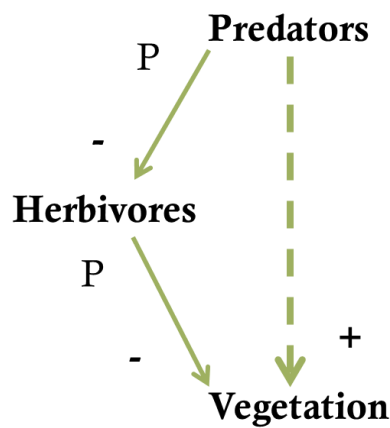
Figure 1: Model of trophic cascade's direct and indirect interactions (Silliman and Angelini, 2012). Note: P denotes predation between trophic levels

Examples of the typical tri-trophic interaction have emerged over recent years, supporting the theory of predator management of herbivores (Hairston et al. 1960; Estes and Palmisano 1974; Estes and Duggins, 1995; Ripple and Larson 2000; Fortin et al. 2005; Silliman and Angelini 2012). Several of these studies show how unregulated herbivory leads to reduction of vegetative species. Typical findings indicate that areas where vegetation diversity and abundance is optimal, predators are maintaining appropriate herbivore populations, whereas areas that are overgrazed have had a predator removed or reduced. This structure has been demonstrated in multiple

aquatic systems including freshwater (Carpenter et al. 1985; Powers 1992) and marine ecosystems (Estes and Palmisano 1974; Wootton 1992).

A notorious example of aquatic trophic cascades can be observed in the kelp beds of the Aleutian Islands and Alaska (Estes and Duggins 1995). Sea otters (*Enhydra lutris*) reduce sea urchin populations through consumption. When sea otters are not present, the sea urchin densities overpower productive kelp beds. This disturbance results in what is known as urchin barrens characterized by low kelp vegetation coverage. As sea otter populations expanded, repopulating former kelp forests, urchin densities declined allowing the kelp beds to grow back. This example provides a demonstration of ecosystem recovery due to the reestablishment of key predators.

Terrestrial trophic cascades can be seen as increasingly complex compared to some of the aquatic trophic cascades. However, they can similarly be applied to food web ecology (Strong 1992) as they can be observed through most major ecological disruptions. For instance, Keesing (1998) noted that ungulates in the east African savanna were impacting the small mammal population. Populations of pouched mice (*Saccostomus meanrsi*) along with eight other small mammal species were disturbed due to increased ungulate populations. The ungulates caused increased habitat disturbance through trampling and consumption, which caused a decrease in vegetative cover. This habitat disturbance resulted in increased predation, decrease in food source, and overall reduction in a suitable habitat for small mammals. Thus, when the ungulate population was disturbed either by naturally lowered densities or through habitat exclusion, the effects cascaded down through the other trophic levels. The correlating trophic levels in this case were the vegetation and, therefore, the small mammal species that inhabited that area (Keesing 1998). Related studies have also been conducted to determine the impact of carnivores on plant

species (Schmitz et al. 2000). Studies were conducted focusing mainly on arthropod carnivore removal, the effects on arthropod herbivores, and, therefore, the direct and indirect effects on plant density and diversity.

It was noted, however, that vertebrate herbivores can have a large impact on plants as well (Huntly 1991) even though few studies have been conducted on this aspect of trophic cascade theory in the northeastern United States. Nonetheless, predation on such vertebrate herbivores is considered to be an important factor in trophic cascade systems, particularly in managing mortality rates among an herbivore species (Messier 1985). However, the area of mammalian trophic cascades is in part lacking, especially pertaining to the Northeast. In particular, the implications of trophic cascade as seen in white-tailed deer (*Odocoileus virginianus*) overabundance are largely unexplored, and require further observation and explanation. A plethora of research pertaining to the many facets of the trophic cascade theory exists, but connections have yet to be made directly linking them to the theory. Research has been conducted on the causes of deer overabundance, as well as the effects on native vegetation, but very little has been researched of the consequences on small mammal populations.

DEER OVERABUNDANCE

Currently, throughout most of the eastern United States, deer are overabundant (Waller and Alverson 1997; DeNicola et al. 2000; Rooney and Waller 2003; Merrill et al. 2003; DeNicola and Williams 2008). Manipulation of woodlands has led to more favorable habitats for deer to flourish and thrive. Agriculture, silviculture, wildlife management and urban sprawl have all played a role in deer expansion (Waller and Alverson 1997). In the early 1920s, in response to the near extirpation of the species, game managers sought to increase populations by imposing

bag limits, gender specific hunting regulations, and creating suitable environments such as edge and early successional habitats (Waller and Alverson 1997; Rooney and Waller 2003).

Overabundance of this species has had severe impacts on native vegetation and associated species. In many reserves, it has been noted that the forest understory is extensively diminished, inhibiting forest regeneration and renewal (McShea et al. 1993; Cote et al. 2004). Both the direct and indirect effects of deer can have serious impacts on forest communities. Damage, browse preference, and deer density are all major components that illicit responses in plant species growth and distribution. Specifically, overbrowsing by deer may limit the regeneration of woody plant species, resulting in a trophic cascade due to habitat modification (Rooney and Waller 2003). In this manner, deer have the ability to completely alter the distribution and abundance of plants, thereby impacting the overall structure of the ecosystem (Waller and Alverson 1997; McShea and Rappole 2000). For example, several studies conducted in Wisconsin revealed that high deer densities resulted in a depressed regeneration of commercially valuable tree species such as willow (*Salix* spp.) and aspen (*Populus* spp.) (Graham 1954; Alverson et al. 1988; Rooney and Waller 2003). However, the magnitude of excessive deer herbivory surpasses individual species, affecting plant populations, communities, and ecosystem processes.

DEER AS PREY

The Northeast is essentially void of apex predators of deer. The cougar (*Puma concolor*) and grey wolf (*Canis lupus*) were noted as primary predators, however, with the historic extirpation of both species, deer densities have grown exponentially, seen in Figure 2 (Boitani 1995; Rooney 2001; Paquet and Carbyn 2003).
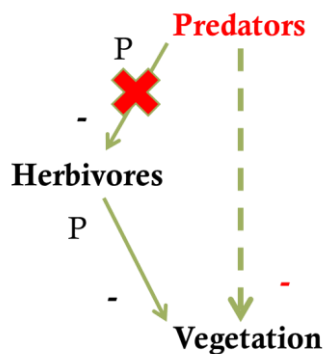
Figure 2: Impact of predator removal on direct and indirect interactions in trophic cascade. Note: P denotes predation between trophic levels

Predator elimination was primarily due to bounty hunting, allowing the deer population to grow largely unchecked. Main predators now consist of eastern coyotes (*Canis latrans* var.), black bears (*Ursus americanus*), and other secondary meso-carnivores that prey on the young, elderly, and wounded deer (Vreeland et al. 2004). Therefore the absence of an apex predator has resulted in a lack of control over deer population surpassing their carrying capacity (McShea 1997).

As a result, hunting regimens have been implemented throughout the Northeast in an attempt to control the continuously growing deer population while providing a form of outdoor recreation. Management of deer populations has proven to be a controversial issue prompting conflict between individuals wanting to reduce the effects of deer on plant species, individuals who believe hunting to be inhumane, and hunters who enjoy the abundance of deer for harvest (Diamond 1992; Diefenbach at el. 1997; McShea et al. 1997; Russel et al. 2001). Unfortunately, hunting alone has been deemed an inadequate means of deer population regulation in many cases (Giles and Findlay 2004; Lebel et al. 2012; Simard et al. 2013; Williams et al. 2013). Although hunting is considered to be one of the most effective removal strategies, deer subjected to lethal

removal often alter their behavior as a result (Williams et al. 2008a). Modifications to the landscape as well as consideration of these reactionary behaviors may improve the efficiency of using sport hunting as a management tool, but currently the management strategy is an insufficient replacement of natural apex predators (Lebel et al. 2012; Williams et al. 2013).

Controlled harvest via sharpshooting has gained recognition as a lethal management strategy. One study used sharpshooting as a means to reduce deer densities in areas were deer-vehicle collisions were prominent (DeNicola and Williams 2008). As a result, deer densities were reduced by up to 76%, with a correlated 78% decrease in deer-vehicle collisions. Deer populations were dramatically reduced due to the controlled harvest in the areas studied.

DEER EFFECTS ON VEGETATION

Along with overabundance, deer are also an opportunistic species that are tolerant of anthropogenic changes to the environment. The lack of natural barriers makes the majority of vegetation accessible to deer populations. As a result, excessive herbivory occurs, causing both native woody and herbaceous plant species to become diminished. Due to preferential browsing and excessive consumption of seedlings, saplings, and dominant herbaceous species, areas with high deer densities have greatly reduced biomass and biodiversity in the forest understory (Webb et al. 1956; McShea et al. 1993; Tierson et al. 1996). This can be further illustrated in Figure 3, indicating the direct effect of increased herbivore predation on the vegetation layer due in part to the indirect effect resulting from an absent apex predator.
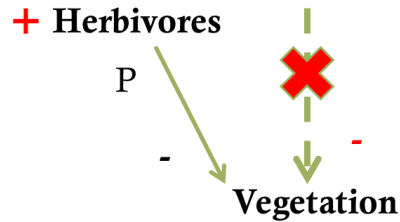
Figure 3: Increased direct effect caused by excessive herbivory causes a reduction in vegetation trophic level when predators are absent. Note: P denotes predation between trophic levels

INTRUSION OF INVASIVE SPECIES

Reduction in biomass of native vegetation has more than just one repercussion. Besides the consequence of lack of native plant density and diversity, a diminished vegetation layer also allows for reduced competition for invasive plant species. Compared to exclosures or fenced areas, regions where vegetation was heavily browsed resulted in the introduction and infestation of invasive plant species (Koh et al. 1996; Williams et al. 2008b). As a result, a dense, invasive vegetation cover has developed in several areas consisting mainly of extremely competitive invasive species such as Japanese barberry (*Berberis thunbergii*), Oriental bittersweet (*Celastrus orbiculatus*), and multiflora rose (*Rosa multiflora*) (Ward et al. 2009).

Invasive plants are considered to be one of the major threats to biodiversity (Rejmánek and Richardson 1996; Anderson et al. 2000; Weber 2003; Gurevitch and Padilla 2004). Moreover, invasive species can cause irreparable damage to an ecosystem by outcompeting native species (Bratton 1982; Harsh et al. 2003; Vilà and Weiner 2004). Previous land use most directly influences the spread of invasive species: human and/or natural disturbances such as agriculture, urban sprawl, horticulture, and habitat fragmentation significantly increases the occurrence of invasive species (Hobbs and Huenneke 1992; Lundgren et al. 2004). In several states including Connecticut, exotic invasive plant species can represent up to 45% of the

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vegetation present (Mehrhoff 2000). Japanese barberry has become one of the most widely known and planted exotic invasive plant species (Silander and Klepeis 1999). This invasive plant, as well as several others, is continuing to expand its range, and in many areas is creating dense monocultures outcompeting native plant species, diminishing biodiversity (Ward et al. 2010, Williams and Ward 2010; Ward and Williams 2011). Figure 4 illustrates the concept of invasive plant species as they overtake and outcompete native vegetation.
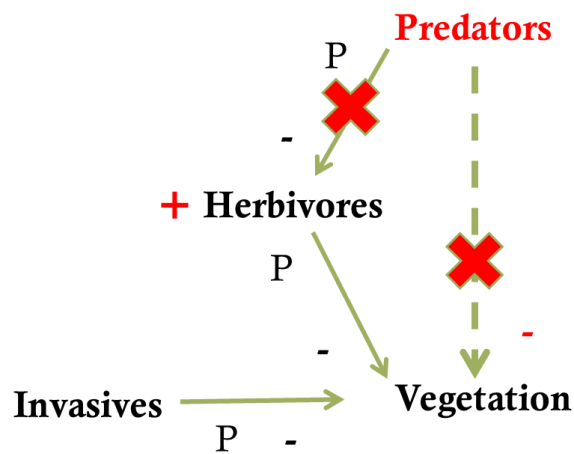
Figure 4: Intrusion of invasive plant species on the disrupted trophic cascade. Note: P denotes predation between trophic levels

JAPANESE BARBERRY

In the early 1900s, Japanese barberry was introduced as an ornamental replacement for common barberry (*Berberis vulgaris*), which was a carrier of black stem grain rust (Thompson 1926). Japanese barberry is now characterized as an extremely invasive plant that has invaded 34 states and 6 Canadian provinces (USDA, NRCS 2014). Japanese barberry alters pH and nitrogen levels in the soil as well as reduces the litter layer in forest understories (Ehrenfeld 1999).

Occasionally it will occur as scattered individuals, but more often as a dense thicket where few other native plant species exist (Kourtev et al. 1998; Ehrenfeld 1999). Japanese barberry is known to not only spread through seed dispersal, but also through a process called layering. Layering occurs as branches of the invasive shrub touch the ground and begin to root forming new plants. Remnants of the roots that persist in the soil can also sprout to form new plants (Zouhar 2008).

Excessive herbivory of competing native plant species, tolerance of low light conditions, and invasive characteristics have combined to aid in the expansion of Japanese barberry thickets throughout Connecticut, as well as other New England states. As seen in Figure 5, Japanese barberry is potentially the most influential of invasive plant species in the northeastern trophic cascade and therefore of particular importance.
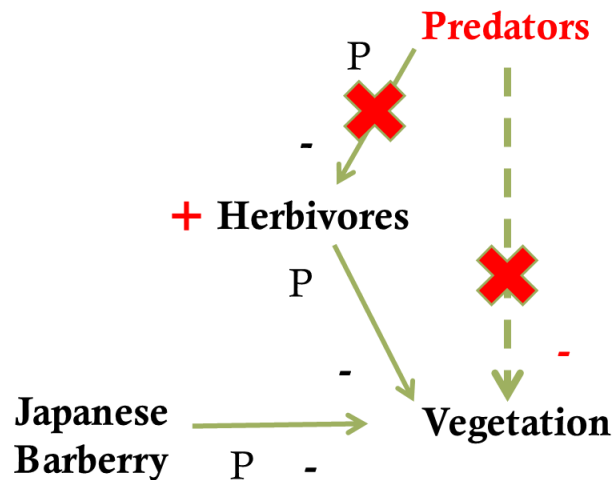
Figure 5: The intrusion of Japanese barberry as the primary invasive plant species disrupting the trophic cascade.

Note: P denotes predation between trophic levels

Approximately 80% of all Lyme disease cases reported in the United States originate from the Northeast and Mid-Atlantic states (Qui et al. 2002). The history of Lyme disease is one of coevolution, as with most obligate parasites (Price 1980). The Lyme disease spirochete, *Borrelia burgdorferi*, requires a vector in order to spread and continue its life cycle. Blacklegged ticks (*Ixodes scapularis*) are the main vector for many other tick-borne diseases such as babesiosis, ehrlichiosis, and encephalitis (Spielman et al. 1985; Telford et al. 1997; Schauber et al. 1998; Stafford et al. 1999; Qiu et al. 2002).

Blacklegged ticks life span is approximately two years. Within those two years they go through four life stages: egg, six-legged larvae, eight-legged nymph, and adults. After they have hatched, they must consume a blood meal at each stage in order to survive and continue development (Centers for Disease Control and Prevention 2011). It's during these feedings that the tick can ingest *Borrelia burgdorferi*, as well as other disease-causing pathogens. As a result, the only stages that are capable of transmitting the various pathogens are the nymphs and adult females, as they are the only stages that undergo a second and third feeding, respectively. At that time, they may have ingested the spirochete from a competent reservoir from their previous blood meals. In subsequent feedings, the tick can transmit the infection to a new host (Stafford 2007; Center for Disease Control and Prevention 2011).

The most common hosts are mice, deer, and humans, as well as other small mammals (Center for Disease Control and Prevention 2011). While human hosts can be greatly impacted through transmission of pathogens, the white-footed mouse (*Peromyscus leucopus*) is the main reservoir. The white-footed mouse shows nominal signs and symptoms when infected with *Borrelia burgdorferi*. The only detection indicating that the mice are infected with the pathogen

causing Lyme disease, is an elevated white blood cell count (Schwanz et al. 2011). The lack of signs or symptoms in conjunction with the species' ability to transmit pathogens through blood meals makes the white-footed mouse a competent reservoir (Richter and Matuschka 2010).

ACARIDES

Use of acaricides, insecticides targeting members of the arachnid Subclass Acari (ticks and mites), can be used to reduce tick densities (Müller et al. 2000). Acaricide dispersion through reservoirs such as white-tailed deer and white-footed mice may aid in reducing tick populations throughout areas where greater densities occur, such as those seen in Japanese barberry infestations.

Mount et al. (1997) conducted computer simulations to determine appropriate management strategies for ticks including acaricides. The study indicated that area-wide use of acaridides, vegetation reduction, or a combination of the two would be an effective short-term solution for residential areas. Additionally, acaricide self-treatment of white-tailed deer would be both a cost-effective and long-term solution to tick and Lyme disease dispersion (Mount et al. 1997; Solberg et al. 2003; Hoen et al. 2009). The simulation also indicated that overall deer reduction would be a beneficial strategy for long term tick decline as well.

Permethrin, a synthetic acaricide, was used in one study to reduce tick densities in wooded areas (Mather et al. 1987). Permethrin-treated cotton was dispersed in areas where white-footed mice were apparent. The mice used the cotton as nesting material, which aided in dispersion of the acaricide. Mice that were in areas containing the acaricide treatment were void of ticks upon collection, whereas those outside the treatment areas were infested. Permethrin is one of the few insecticides recommended for direct application as a repellent in the Northeast (Stafford 2007).

Novel ecosystems, also referred to as emerging ecosystems, consist of new species density and diversity in a given biome (Milton 2003; Hobbs et al. 2006). Hobbs et al. (2006) stated that novel ecosystems are characterized by two traits: a new species combination that may alter ecosystem functioning, and a human origin, whether deliberate or inadvertent. Mainly, the ecosystem was altered or converted by human actions causing new combinations and interactions between species and their environment. These causes originate primarily from human sources such as introduction of invasive species, land modification, agricultural use, fragmentation, etc. (Hobbs et al. 2006; Hobbs et al 2009; Hobbs et al. 2013).

Many ecosystems have been transformed in non-historical configurations due to both biotic and abiotic factors (Hobbs et al. 2009). As a result, these novel ecosystems occupy a zone in the middle of "natural" and "wild" (Hobbs et al. 2003). Several of these novel ecosystems are revealed to be hybrid systems, in which a portion of the original cascade remained the same with the addition of several novel elements (Hobbs et al. 2006). Consequently, these novel ecosystems do not respond as readily to traditional management strategies. Stemming from this theory will be an introduction of new approaches to conservation restoration and environmental management. Primarily, strategies will be in response to these ecosystems that offer critical, non-historical ecosystem functions or are simply immune to typical restorative efforts (Hobbs et al. 2013).

RESEARCH.

Trophic cascades are highly influential interactions that ripple through ecosystems influencing both density and diversity of correlated species. Furthermore, these cascades can impact the entire functionality of an ecosystem-causing novel and hybrid forms to arise. Although they were once considered to be rare occurrences, rising interest has established that

trophic cascades occur across a variety of habitats, both terrestrial and aquatic. However, there is still much to learn about the subject and a wide variety of models yet to be explored. Failure to acknowledge and fully understand the simultaneous top-down and bottom-up processes of these cascades may result in the diminishment of diverse landscapes and communities. This denotes the main purpose of this study; an investigation and explanation of the northeastern trophic cascade.

While there is a copious amount of research being conducted on the various levels of the northeastern ecosystem described previously, very little has been studied on the overall application of the trophic cascade theory in the Northeast as it applies to deer populations. Figure 6 illustrates the increasing complexity of the Northeastern cascade as the effects of extirpated apex predators ripple through multiple trophic levels. In this particular study, the effects of the trophic cascade will be explored down to small mammals and blacklegged ticks. Essentially, my research will show the relationship between all these trophic levels and how deer as a result of absent apex predators directly and indirectly influence small mammals and black legged ticks. Furthermore, the results of this research may provide insight into appropriate management strategies and applications for deer as well as the trophic levels that their overabundance may be affecting. Overall, the science of trophic cascades will aid in conducting informed management, conservation, and restoration decisions for an abundance of ecosystem, but specifically those seen in the Northeast.
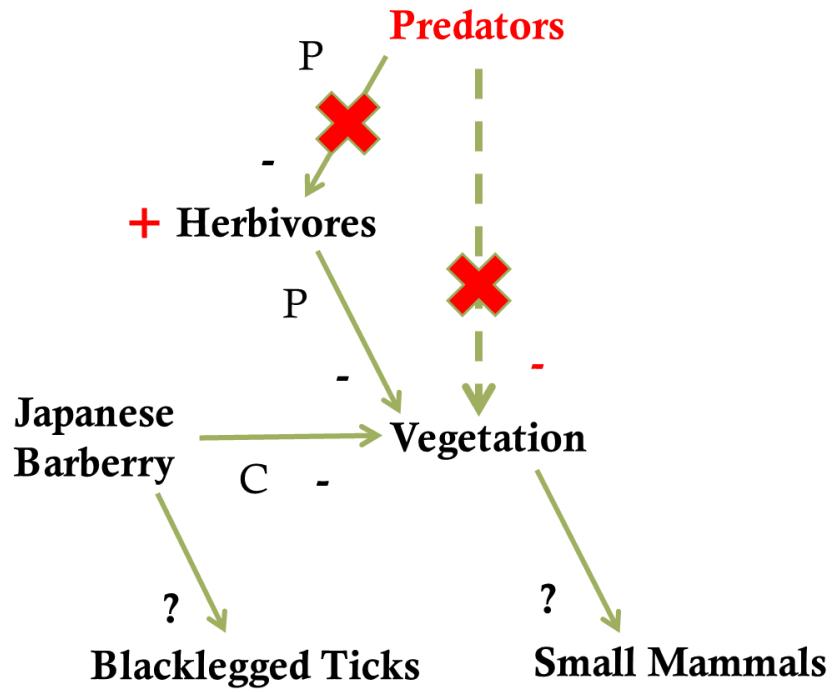
Figure 6: The top-down effects of an absent apex predator on small mammals and blacklegged ticks. Note: P denotes predation between trophic levels, and C denotes competition.

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CHAPTER 2

TROPHIC CASCADE EFFECTS OF DEER OVERABUNDANCE ON CONNECTICUT'S NATIVE VEGETATION
AND SMALL MAMMAL POPULATIONS: THEORY AND MANAGEMENT

INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) population of southern New England has

grown exponentially over the past century due largely to the absence of apex predators (Rooney

2001; Beschta and Ripple 2009; Ripple and Beschta 2012). Deer overabundance has had serious

impacts to numerous facets of such ecosystems, referred to as trophic cascade theory. This theory

describes how the destabilization of one trophic level results in both the direct and indirect

disruption of other subsequent levels (Beckerman et al. 1997; Pace et al. 1999; Schmitz et al.

2004; Terborgh and Estes 2012). In the Northeast, the extirpation of secondary consumers,

specifically mountain lions (*Felis concolor*) and grey wolves (*Canis lupus*), has resulted in an

overabundance of primary consumers (deer). This has resulted in excessive herbivory impacts,

reducing native plant species diversity and abundance throughout their range (Webb et al. 1956;

Alverson et al. 1988; deCalesta and Stout 1997; Eschtruth and Battles 2008; Williams et al.

2009).

Herbivory impacts to grass and shrub layers from overabundant herbivores has had

negative impacts to small mammal habitat, thus reducing population abundance. Keesing (1998)

documented that increased abundances of ungulates in the east African savanna were negatively

impacting small mammal abundance. Populations of pouched mice (*Saccostomus meanrsi*) along

with eight other small mammal species were significantly reduced due to increased ungulate

abundances (Keesing 1998). Ungulates caused increased habitat disturbance through trampling

and herbivory, which caused a decrease in vegetative cover resulting in increased rates of

predation, decreased food resources, and overall habitat reduction for small mammals (Keesing 1998).

The trophic cascade impacts of the reintroduction of an apex predator, the grey wolf, are beginning to restore the greater Yellowstone ecosystem to what it was prior to their extirpation (Ripple and Larsen 2000). With their reintroduction, the balance of trophic levels is being restored to its original, intact state through direct predation, provision of an addition food sources for scavengers (carrion), reduction of mesopredators, landscape modification, as well as additional alterations to the environment (Smith et al. 2003; Ripple and Beschta 2004). In particular, the reintroduction of wolves has caused a reduction in herbivore abundance, specifically elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*). The reduction in primary consumers and resulting decreased herbivory impacts caused an increase in vegetative growth, predominantly willow (*Salix* spp.) and aspen (*Populus tremuloides*) (Smith et al. 2003; Ripple and Beschta 2012). The restoration of wolf populations has led to an increase in growth in several aspen stands by means of elk redistribution (Ripple et al. 2001), causing a transformation in the landscape and environment.

In addition to increasing the native vegetation layer, mesopredator prevalence has been reversed in the presence of wolves (Miller et al. 2012). Decreased numbers of coyotes (*Canis latrans*) have been reported, which benefits small mammals such as rodents and lagomorphs (Ripple at al. 2013). Consequently, small mammal populations increased in response to decreased mesopredator presence and an increase in vegetative cover caused by decreased elk herbivory (Miller et al. 2012). Essentially, these studies link carnivores, herbivores, plants, and small mammals and how they are influenced through a similar trophic cascade; the removal of an apex predator.

Generally in southern New England, excessive herbivory would result in the loss of ground cover, which would result in a decline in small mammal populations, such as white-footed mice (*Peromyscus leucopus*), that require such vegetation for food and predator avoidance (Adler and Wilson 2004). However, in disturbed, abandoned agricultural lands, that comprises much of the Northeast, the intrusion of invasive plant species such as Japanese barberry (*Berberis thunbergii*), Oriental bittersweet (*Celastrus orbiculatus*), and multiflora rose (*Rosa multiflora*) destabilizes the normal trophic cascade (Koh et al. 1996; Elias et al. 2006; Williams et al. 2009). Excessive deer herbivory has caused a significant reduction in native plant species allowing little to no competition for invasive species (Williams et al. 2008b; Cipollini et al. 2009; Williams et al. 2009; Ward et al. 2013). As a result, unpalatable invasive species are able to flourish in the absence of native species and in presence of overabundant deer thereby establishing a vegetation layer.

Invasive plants are considered to be one of the major threats to global biodiversity (Rejmánek and Richardson 1996; Anderson et al. 2000; Weber 2003; Gurevitch and Padilla 2004). Moreover, invasive species can cause irreparable damage to an ecosystem by outcompeting native species (Bratton 1982; Harsh et al. 2003; Vilà and Weiner 2004). Previous land use most directly influences the spread of invasive species: human and/or natural disturbances such as agriculture, urban sprawl, horticulture, and habitat fragmentation significantly increase the occurrence of invasive species (Hobbs and Huenneke 1992; Lundgren et al. 2004). In several states including Connecticut, exotic invasive plant species represent up to 45% of the vegetation present (Mehrhoff 2000). Japanese barberry has become one of the most widely known and planted exotic invasive plant species (Silander and Klepeis 1999). This invasive plant, as well as several others, is continuing to expand its range, and in many areas is

creating dense monocultures outcompeting native plant species, thus diminishing biodiversity (Ward et al. 2010, Williams and Ward 2010; Ward and Williams 2011).

In the early 1900s, Japanese barberry was introduced as an ornamental replacement for common barberry (*Berberis vulgaris*), which is a carrier of black stem grain rust, which is a threat to the grain industry (Thompson 1926). Japanese barberry is now characterized as an extremely invasive plant that has invaded 34 states and 6 Canadian provinces (USDA, NRCS 2014) and will occasionally occur as scattered individuals, but more often as a dense thicket where few other native plant species exist (Kourtev et al. 1998; Ehrenfeld 1999). Excessive herbivory of competing native plant species, tolerance of low light conditions, and invasive characteristics have combined to aid in the expansion of Japanese barberry thickets throughout Connecticut, as well as other New England states. The relationship between trophic levels has the potential to effect correlating trophic levels as well, but to what extent remains unknown.

However, in two studies conducted in Maine, blacklegged tick abundances were notably higher in areas were Japanese barberry was present (Lubelczyk et al. 2004; Elias et al. 2006). Similar research in Connecticut (Williams et al. 2009, Williams and Ward 2010) indicated greater densities of blacklegged ticks as well as a higher prevalence of *Borrellia burgdorferi* in ticks in areas where barberry was present compared to those where it was absent or managed. However, very little has been examined as to the state of the primary reservoir; white-footed mice.

White-footed mice infected with *B. burgdorferi* are largely asymptomatic. In one study, both activity and levels of white blood cells were unaffected in mice infected with *B. burgdorferi* (Schwanz et al. 2011). The only physiological change witnessed that would indicate mice were

infected with the pathogen was the production of antibodies to *B. burgdorferi* (Schwanz et al. 2011). However, when humans become infected with *B. burgdorferi*, a host of signs and symptoms appear in skin manifestations such as red blotches and circles (aka. *Erythema migrans*) to fatigue, headaches, fever, achiness, and chills (Steere et al. 1983). For vector-borne illnesses, the relationship between reservoir host, pathogen, and vector play an essential role in the transmission of the disease-causing pathogens. Unlike humans, white-footed mice allow for *B. burgdorferi* to spread without altering their behavior or physiology, making the species a perfect means for transmittance.

A plethora of research exists pertaining to the many facets of trophic cascade theory in the Northeast, but connections have yet to be made directly linking ecological data to the theory. Research has been conducted on the causes of deer overabundance, as well as its effects on native vegetation, but little has been studied on the resulting impacts to small mammal populations as well as blacklegged ticks. This is of particular importance as they have the potential to negatively affect public health as the main reservoir and vector, respectively, for *B. burgdorferi* (Williams et al. 2009, Williams and Ward 2010). Therefore, the objective of this research was to determine the effects of invasive plant species, namely Japanese barberry, on trophic cascades in the Northeast, which may provide insight into appropriate management strategies for both plants and wildlife associated with this cascade in the future.

This study will attempt to further define the trophic cascade in the Northeast and whether it is impacted by the intrusion of invasive plant species, in particular Japanese barberry. Furthermore, the research conducted attempts to determine the downward effect on small mammals with three competing hypotheses: small mammal populations will increase in areas where Japanese barberry is present; small mammal populations will remain the same both in the

presence and absence of Japanese barberry; finally, small mammal populations will decline in areas where Japanese barberry is absent. Concurrently, the impact on blacklegged ticks and the associated *B. burgdorferi* will be compared between plots as well.

STUDY AREAS

Three replicate study areas were established in geographically separate areas: one on South Central Connecticut Regional Water Authority property (North Branford; 41.373145, -72.771793), one in the town of Redding on the Centennial Watershed State Forest, which is jointly managed by the Aquarion Water Company, The Nature Conservancy, and the Connecticut Department of Energy and Environmental Protection (Redding; 41.284047, -73.367029), and one in northeastern Connecticut on the University of Connecticut Forest (Storrs; 41.824050, -72.252106). All study areas had remnant stone walls running throughout and were once agricultural fields or pastures; Storrs and the North Branford study areas were abandoned in the early 1900s, as were the Redding study areas in the 1940s.

Because of low light conditions due to intact upper canopies and browse damage caused by exceedingly high white-tailed deer populations (upwards of 40 deer/km^2) (Williams and Ward 2006), there was virtually no native shrub species on study sites except northern spicebush (*Lindera benzoin*) (Williams et al. 2009). In addition, the invasive wine raspberry (*Rubus phoenicolasius*), multiflora rose, and burning bush (*Euonymus alatus*) were also present in the understory. All study areas had medium to dense stands of mature Japanese barberry that dominated the understory and excluded desirable forest regeneration and native herbaceous vegetation. Further details on stand histories, forest composition, soil types, and local climate can be found in Ward et al. (2009).

METHODS

Plot Design

Three treatment plots were established at each study area, which included an intact barberry infestation where barberry was not controlled (full barberry), an area where barberry was managed by a series of control methods (managed barberry), and an area where barberry was minimal or absent (no barberry). No barberry areas were located within the adjacent areas and were similar in stand composition as the other two treatment areas, but had limited or no barberry in the understory.

Initial control of barberry was accomplished by mechanical cutting and shredding of the above-ground portion of the plant and was completed in March 2007. We used a hydraulically driven rotary wood shredder (Model# BH74FM, Bull Hog®, Fecon Inc., Lebanon, OH) mounted to a compact track loader (Model# T300, Bobcat®, West Fargo, ND) for initial control. Barberry clumps missed by the wood shredder (adjacent to trees, stone walls, or large rocks) were hand cut. Follow-up methods used to control new ramets (sprouts) were: directed flame with a 100,000 BTU backpack propane torch (Model# BP 223 C Weed Dragon, Flame Engineering, Inc., LaCrosse, KS), foliar application of glyphosate, and triclopyr. Follow-up control methods were applied separately on sub-plots within habitat plots, but for the purposes of this study, the entire habitat plot with multiple control methods were considered a single "managed" habitat. Follow-up control methods were completed in late June 2007. More details on specific control methods can be found in Ward et al. (2009).

Vegetation

Cover at each sample point was measured using a 0.25 m^2 sampling frame with 16 cells. For this study, cover at each sample point was defined as the proportion of 16 cells within the sampling frame that had at least one live barberry stem or leaf. For example, if barberry was

observed in seven cells, then barberry cover was 7/16 (44%). This method, while biased to give slightly higher estimates than traditional cover estimates, especially for low density patches, is reproducible and can be used in both dormant (leaf-off) and growing seasons (Ward et al. 2013).

Mouse Trapping

Mice were trapped annually using folding Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) from June – September 2007 - 2013. Twenty traps were set in permanent grids with 15 m spacing at each of the three treatment plots (n = 60) at each replicate study area and baited with peanut butter. Captured mice were temporarily sedated using the inhalant anesthetic isofluorane. Each mouse then received a uniquely numbered ear tag (National Band and Tag Co., Newport, KY) and the number of larval ticks feeding on mice was recorded without removal.

Sedated mice were allowed to recover from the effects of isofluorane and were released into the plot from which they were originally captured. Mouse capture and handling protocols were approved by the Wildlife Division of the Connecticut Department of Energy and Environmental Protection (#816005) and The Connecticut Agricultural Experiment Station's Institutional Animal Care and Use Committee (P18-13) in accordance with the American Society of Mammalogists guidelines for the use of wild animals in research (Sikes and Gannon 2011).

Based on pelage and morphological characteristics, it was assumed that all captured mice were white-footed mice rather than deer mice (*Peromyscus maniculatus*). While deer mice are difficult to distinguish from white-footed mice based on appearance, the known range of deer mice in Connecticut is restricted to the northwestern portion of the state (DeGraaf and Rudis 1986), which was outside our study areas.

Adult Tick Sampling

A 1 m^2 white canvas cloth attached to a dowel was used to flag vegetation on the forest floor over established transects totaling 200m in each treatment. Flags were checked for ticks every 15m. Gathered ticks were relocated to a laboratory, stored in a hydrator, and incubated at 10ºC. One-way ANOVA was used to determine differences in adult tick counts between treatments for each sampling interval. Tukey HSD was used to maintain alpha levels at $P < 0.05$ for multiple comparison tests of differences between treatments.

Borrelia burgdorferi Testing and Health Risk

Gathered tick midguts were dissected under a stereo microscope and contents were smeared on 12 well glass microscope slides (# 30-103HTC, Thermo Fisher Scientific, Portsmouth, NH). *Borrelia burgdorferi* spirochetes were identified in midgut contents by using indirect fluorescent antibody (IFA) staining methods with monoclonal antibody H5332, which is specific for outer surface protein A of *B. burgdorferi* (Magnarelli et al. 1994). Fluorescein isothiocyanate-conjugated goat anti-mouse immunoglobulins (KPL, Inc., Gaithersburg, MD) were diluted 1:40 in phosphate-buffered saline solution and used as the second antibody. Procedural details followed established protocols (Anderson et al. 1991, Magnarelli et al. 1994, Magnarelli et al. 1997).

In order to assess relative risk to public health, the estimated density of *B. burgdorferi*-infected ticks/ha was determined for each of the three treatments by taking the product of infection prevalence (%) and relative tick density (including nymphs for Fall 2008) for each sampling interval. One-way ANOVA was used to determine differences in relative density of infected ticks between treatments for each sampling interval. Tukey HSD was used to maintain alpha levels at $P < 0.05$ for multiple comparison tests of differences between treatments.

Population Estimations

      Program MARK was used to provide parameter estimates for closed and open populations. Estimates are produced from reencounters with marked animals through resighting, live recaptures, or dead recoveries (White and Burnham 1999). Time intervals between encounters were not even and therefore, were adjusted for each occasion. There were three attributes for each group of small mammals modeled; full barberry, no barberry, and managed barberry. Population estimates and survival rates were produced for each attribute group from the year 2007 to 2013. A POPAN Jolly-Seber (JS) model was used for population estimates and Live-Recaptures Only Cormack Jolly-Seber (CJS) model was used for survival rates. POPAN was selected as it provides a robust parameterization of the JS model (Schwarz and Arnason 1996). The protocol and assumptions for the JS model are very similar to the CJS model. On each sampling occasion an animal is captured and tagged with individually identifiable tags and then released. In this case, small metal ear tags engraved with a number were utilized. Previously marked animals have their numbers recorded and are then released. For POPAN, the assumption of equal catchability of marked and unmarked animals is required to estimate abundance, recruitment and population growth. Additional assumptions for both models include all animals retain their tag through the experiment, tags are read properly, sampling is instantaneous, survival probabilities are the same for all animals between each pair of sampling occasions, and the study area is constant (Cooch and White 2006). The experiment also assumes an open population where animals may leave the population by death or emigration. Animals may also enter the population through immigration or recruitment (birth) (Krausman and Cain 2013).

      Schwarz and Arnason (1996) parameterized the JS model in terms of a super-population (N) and the probability of entry (pent). Parameter index matrices (PIMs) were constructed to phi (apparent survival), p (capture probability), pent (probability of entry into the population per

occasion) and N (super-population size). The Mlogit link function was implemented to provide a constraint on the pent parameter. Mlogit link enables the sum of the pent parameters ≤ 1.

The POPAN model within MARK was run using adjusted time intervals as trapping events within each year differed in frequency and duration. Three attribute groups were used to account for the areas of no barberry, full barberry, and managed barberry for each year. The parameter specific link function was used to parameter outputs. Sin was used for Phi parameters and logit for pent parameters. N, the super-population, used the Log function as it was not restricted to a value between 0 and 1. Estimated population size, N, and net births were acquired in the derived parameter section of the model.

The Cormack Jolly-Seber model was also adjusted to meet the species sample size. The same modifications were used for time intervals and attribute groups as POPAN models. To adjust for over dispersion, the variance inflation factor, also known as c-hat was adjusted to be a value other than 1. The c-hat was calculated by running a global model to determine deviance and dividing the value by the mean deviance of the cumulative bootstrap simulations. The models were averaged by location and year to accommodate the variations.

One way-ANOVA was used to determine differences population size and survival rates between treatment, years, and locations. Tukey HSD was used to maintain an alpha of $P < 0.05$ for multiple comparison tests.

RESULTS

Mouse trapping in the years 2007, 2009, 2010, 2011, and 2012 minimal disturbance was observed in traps. Few traps were triggered prematurely and/or moved several meters from their original location; most likely due to raccoons (*Procyon lotor*). For those years, equal disturbance

was assumed across all treatments and locations except for Redding site in 2009. Major trap

disturbance occurred at the Redding site resulting in unusable data for mouse population and

survival rate estimates. The removal of this data works under the assumption that there were

insufficient data to run the model under Program MARK. This was concluded as two other

estimates were removed from the final data set in Tables 1 and 2. The insufficient data resulted

in the model producing outliers for these two sampling intervals. Outliers were indicated as lying

outside two standard deviations of the mean for that location.

Mouse Populations and Survival Rates
       There was no significant difference in abundance of white-footed mice between

treatments ($F = 0.022$; df =2; $P = 0.979$). There was also no significant difference in abundance

between years of sampling ($F = 0.844$; df = 4; $P = 0.507$). However, there was a significant

difference between study locations ($F = 3.949$; df = 2; $P = 0.028$). Refer to Tables 1-3 for

population estimates.

       Similarly, there was no significant difference in survival rates of white-footed mice

between treatments ($F = 2.140$; df = 2; $P = 0.122$). There was also no significant difference in

survival rates between locations ($F = 1.591$; df = 2; $P = 0.208$) or between years ($F = 1.649$; df =

4; $P = 0.166$). Refer to Tables 4-12 for survival rates.

Adult Tick Sampling
       There was no significant difference in tick density by year ($F = 1.363$; df = 6; $P =$

0.245). However, there was a significant difference by location ($F = 7.636$; df = 2; $P = 0.001$).

Ticks sampled in Redding and North Branford were significantly greater in density than those

sampled in Storrs. Tick densities were also significantly greater in full barberry treatments

compared to both managed and no barberry treatments (F = 17.280; df = 2; P = 0.000). Refer to Tables 13-15 for tick densities.

Borrelia burgdorferi Testing and Health Risk

There was no significant difference in infected tick density by year (F = 1.713; df = 6; P = 0.135). However, there was a significant difference in infected tick density by location (F = 6.507; df = 2; P = 0.003). Ticks collected in Redding and North Branford had significantly greater infected tick densities than ticks collected in Storrs. Additionally, there was a significant difference in infected tick density by treatment (F = 14.836; df = 2; P = 0.000). Full barberry was significantly greater compared to managed barberry and no barberry treatments. Refer to Tables 16–21 for infected tick densities.

Vegetation Surveys**.**

Cover of Japanese barberry was not significantly different between locations (F = 2.972; df = 2; P = 0.059) or between years (F = 0.030; df = 6; P = 1.000). However, there was a significant difference in barberry cover between barberry treatment areas (F = 94.549; df = 2; P = 0.000): full barberry areas averaged 46.1% (+/-1.2%) cover, managed barberry 4.1% (+/-0.3%), and no barberry areas 2.4% (+/-0.3%). Refer to Tables 22-24 for percent cover.

DISCUSSION

While there was no significant difference in white-footed mouse abundance by treatment or by year, there was a significant difference in abundance between study locations statewide (Tables 1-3). This can be attributed to a multitude of factors, including but not limited to climate, human development, predator density, and other variables that would require further investigation. These results are quite novel in respect to prior trophic cascade research. Similar studies in South Africa and Yellowstone National Park have shown that increased densities of apex predators resulted in an increased density of small mammals, such as mice (Keesing 1998;

Ripple and Beschta 2004; Ripple and Beschta 2012). Conversely, a decrease in predator abundance resulted in a corresponding decrease in small mammal populations (Keesing 1998; Smith et al. 2003; Ripple and Beschta 2004; Ripple and Beschta 2012). In the previously disturbed ecosystems of the Northeast, there may be alternate or additional trophic cascades in effect.

This may indicate that the intrusion of invasive plant species such as Japanese barberry may disrupt the original trophic cascade. Although it is possible that previous studies had sites containing invasive plant species as well, Japanese barberry is an overly competitive species that dominates the vegetation layer of woodland habitats (Silander and Kelpeis 1999). Therefore, the presence of this invasive species may have altered the trophic cascade effects caused by the absence of an apex predator, resulting in a limited effect on small mammal populations. There was also no significant difference in survival rates between locations, years, and treatments, indicating that the trophic cascade did not affect the small mammal populations, specifically white-footed mice.

In Connecticut, trophic levels above the primary producer (the vegetation layer) were all impacted by the absence of an apex predator. Deer populations were reported to be approximately 40 individuals per km^2 at North Branford (Williams and Ward 2006). This population density was high, due to the deficiency of a sufficient apex predator to control both size and distribution of the deer. As a result, native vegetation was diminished, and unpalatable invasives plant species maintained high percent cover over all three sites (Table 22-24). While trophic cascade impacts on small mammals were insignificant in these plots, there was a corresponding increase in blacklegged tick abundance.

Blacklegged tick densities were significantly greater in areas of full barberry compared to no barberry and managed barberry (Tables 13-15). Furthermore, with infection prevalence similar in ticks between treatments, there was significantly more *B. burgdorferi*-infected ticks in areas of full barberry compared to plots containing no barberry or managed barberry (Tables 15-21).

It would seem that the layer of invasive plant species, specifically Japanese barberry, may be where the disruption in the original cascade occurred. This has resulted in a fluctuation in blacklegged tick populations and associated Lyme disease risk, while leaving small mammal populations abundances unaltered. These results may indicate that the trophic cascade occurring as a result of deer overabundance differs in disturbed areas of the Northeast compared to those seen in studies in greater Yellowstone ecosystems and in Africa.

The results of this study may indicate that the Northeast harbors a novel ecosystem. Due to the abundance and persistence of invasive plant species, a trophic cascade may have been altered. Consequently, the small mammal trophic level that would normally have been disrupted in this particular cascade has remained unaffected, while different species have been disturbed. Many ecosystems have been similarly transformed in non-historical configurations due to both biotic and abiotic factors (Hobbs et al. 2009). In this case, the biotic factor causing this rapid transformation is invasive plants. This study may have revealed a hybrid system, in which a portion of the original cascade remained the same (primary and secondary consumers) with the addition of several novel elements (primary producers) (Hobbs et al. 2006). From this perspective, a new or varied approach may be required to restore the ecosystem to its original state. Traditional and/or historical approaches to management, such as the ones implemented in Yellowstone (Ripple et al. 2001; Smith et al. 2003; Ripple and Beschta 2004), may not be

appropriate for the northeastern ecosystem. Removal and management of the primary invasive Japanese barberry (Ward et al 2009; Ward et al. 2010; Williams and Ward 2010) may prove to be an effective strategy for restoring the original cascade in addition to deer management (DeNicola and Williams 2008).

Furthermore, the increase in *B. burgdorferi*-infected ticks is also of great significance and public health concern. The research conducted in this study may provide insight into a new approach to Lyme disease management by exposing the main reservoir, white-footed mice, as a stable factor between plots, unlike tick populations. In that respect, perhaps direct management of ticks and Japanese barberry, as opposed to reservoir management would be the most effective strategy.

Removal of Japanese barberry is one possible strategy for reducing the public health concern of Lyme disease, as indicated by the results of this study. The difference between no barberry and managed barberry plots' tick densities and infected tick densities were negligible. Therefore the reduction in Japanese barberry biomass in managed areas resulted in a significant decrease in *B. burgdorferi*-infected ticks partially by eliminating questing habitat (Williams et al. 2009). Furthermore, the diminished invasive shrub layer returned microclimatic conditions to their original state, whereas full barberry areas maintained a temperature and humidity level that is more favorable to tick survival (Williams and Ward 2010). The management and reduction of Japanese barberry can play an essential role in reducing the threat of tick-borne illnesses to members of the public.

Use of acaricides, insecticides targeting members of the arachnid Subclass Acari (ticks and mites), may be encouraged to reduce tick densities as well (Müller et al. 2000). Acaricide

dispersion through reservoirs such as white-tailed deer and white-footed mice may aid in diminishing tick populations throughout areas where greater densities occur, such as those seen in Japanese barberry. One study conducted computer simulations to determine appropriate management strategies for ticks including acaricides (Mount et al. 1997). The study indicated that area-wide use of acaridides, vegetation reduction, or a combination of the two would be an effective short-term solution for residential areas. Additionally, acaricide self-treatment of white-tailed deer would be both a cost-effective and long-term solution to diminish tick and Lyme disease dispersion (Mount et al. 1997; Solberg et al. 2003; Hoen et al. 2009). The simulation also indicated that overall deer herd reduction would be a beneficial strategy for long term tick decline as well.

Overall, this study may have exposed a novel ecosystem with a variation of a trophic cascade that is widely studied seen in parts of both Yellowstone and Africa. The novel ecosystem may be composed of a disrupted or additional cascade. Therefore, the establishment of a hybrid ecosystem in the Northeast may provide an interesting new model for wildlife management. The research conducted on this trophic cascade may afford new insight into habitat restoration as well as wildlife and disease management. Hopefully, the findings of this research will aid in rectifying the disruption in the Northeast environment that has led to a disturbed cascade and an increase in blacklegged ticks infected with *Borrelia burgdorferi*.

Table 1. Population estimates (SEM) for white-footed mice per hectare in Redding, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	85.1 (7.0)	122.5 (3.6)	71.7 (2.7)
2008	-	-	-
2009	-	-	-
2010	74.3 (4.3)	64.5 (3.9)	65.6 (3.9)
2011	74.4 (2.0)	111.1 (5.4)	637.4*
2012	59.9 (1.8)	30.2 (1.4)	48.4 (1.9)
2013	-	-	-

*Statistically significant outlier

Table 2. Population estimates (SEM) for white-footed mice per hectare in North Branford, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	81.5 (1.2)	58.0 (1.2)	91.6 (1.8)
2008	46.1 (0.4)	38.9 (0.5)	68.8 (1.5)
2009	-	-	-
2010	41.3 (0.9)	53.3 (0.4)	64.9 (1.4)
2011	62.0 (1.6)	70.7 (1.9)	111.8 (3.8)
2012	64.3 (2.7)	513.4*	81.4 (1.0)
2013	-	-	-

*Statistically significant outlier

Table 3. Population estimates (SEM) for white-footed mice per hectare in Storrs, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	43.8 (1.2)	37.5 (5.9)	60.7 (3.0)
2008	90.0 (2.8)	63.1 (0.8)	49.6 (3.1)
2009	-	-	-
2010	39.7 (0.6)	45.2 (0.9)	25.9 (0.0)
2011	33.9 (0.3)	30.4 (0.3)	34.4 (1.1)
2012	90.9 (3.1)	74.9 (3.3)	28.9 (1.3)
2013	-	-	-

Table 4. Survival rate (SEM) of white-footed mice between sampling occasions in managed barberry in Redding, CT.

Year	1	2	3	4
2007	0.77 (0.09)	0.75 (0.09)	0.77 (0.09)	0.75 (6.41)
2008	-	-	-	-
2009	-	-	-	-
2010	0.82 (0.06)	0.83 (0.07)	0.85 (2.41)	-
2011	0.88 (0.07)	0.82 (0.08)	0.86 (1.82)	-
2012	0.86 (0.05)	0.86 (0.05)	0.86 (5.21)	-
2013	-	-	-	-

Table 5. Survival rate (SEM) of white-footed mice between sampling occasions in full barberry in Redding, CT.

Year	1	2	3	4
2007	0.90 (0.05)	0.88 (0.05)	0.89 (0.06)	0.89 (6.38)
2008	-	-	-	-
2009	-	-	-	-
2010	0.82 (0.06)	0.83 (0.07)	0.86 (2.41)	-
2011	0.85 (0.08)	0.80 (0.09)	0.84 (2.28)	-
2012	0.86 (0.05)	0.87 (0.05)	0.86 (5.22)	-
2013	-	-	-	-

Table 6. Survival rate (SEM) of white-footed mice between sampling occasions in no barberry in Redding, CT.

Year	1	2	3	4
2007	0.86 (0.07)	0.84 (0.07)	0.85 (0.08)	0.85 (6.40)
2008	-	-	-	-
2009	-	-	-	-
2010	0.83 (0.06)	0.84 (0.07)	0.86 (2.42)	-
2011	0.66 (0.24)	0.60 (0.34)	0.64 (1.99)	-
2012	0.86 (0.05)	0.87 (0.04)	0.86 (5.22)	-
2013	-	-	-	-

Table 7. Survival rate (SEM) of white-footed mice between sampling occasions in managed barberry in North Branford, CT.

Year	1	2	3	4
2007	0.93 (0.05)	0.83 (0.05)	0.72 (0.09)	0.81 (2.19)
2008	0.89 (0.05)	0.88 (4.08)	-	-
2009	-	-	-	-
2010	0.85 (0.07)	0.91 (0.04)	0.85 (6.10)	-
2011	0.87 (0.05)	0.77 (0.06)	0.88 (9.00)	-
2012	0.86 (0.05)	0.86 (0.05)	0.86 (5.46)	-
2013	-	-	-	-

Table 8. Survival rate (SEM) of white-footed mice between sampling occasions in full barberry in North Branford, CT.

Year	1	2	3	4
2007	0.93 (0.05)	0.83 (0.05)	0.72 (0.09)	0.81 (2.19)
2008	0.88 (0.05)	0.87 (3.99)	-	-
2009	-	-	-	-
2010	0.85 (0.06)	0.91 (0.04)	0.85 (6.09)	-
2011	0.89 (0.05)	0.77 (0.06)	0.89 (8.98)	-
2012	0.86 (0.05)	0.87 (0.05)	0.86 (5.47)	-
2013	-	-	-	-

Table 9. Survival rate (SEM) of white-footed mice between sampling occasions in no barberry in North Branford, CT.

Year	1	2	3	4
2007	0.93 (0.05)	0.83 (0.04)	0.72 (0.09)	0.81 (2.19)
2008	0.89 (0.05)	0.87 (4.05)	-	-
2009	-	-	-	-
2010	0.85 (0.06)	0.91 (0.04)	0.85 (6.10)	-
2011	0.89 (0.05)	0.78 (0.05)	0.90 (10.55)	-
2012	0.86 (0.05)	0.87 (0.04)	0.86 (5.46)	-
2013	-	-	-	-

Table 10. Survival rate (SEM) of white-footed mice between sampling occasions in managed barberry in Storrs, CT.

Year	1	2	3	4
2007	0.95 (0.04)	0.98 (0.02)	0.77 (0.08)	0.93 (6.11)
2008	0.65 (0.09)	0.91 (0.03)	-	-
2009	-	-	-	-
2010	0.93 (0.05)	0.84 (0.07)	0.96 (7.49)	-
2011	0.91 (0.05)	0.91 (0.05)	0.91 (0.05)	-
2012	0.73 (0.09)	0.74 (0.09)	0.74 (1.60)	-
2013	-	-	-	-

Table 11. Survival rate (SEM) of white-footed mice between sampling occasions in full barberry in Storrs, CT.

Year	1	2	3	4
2007	0.95 (0.06)	0.97 (0.04)	0.77 (0.10)	0.93 (6.13)
2008	0.99 (0.00)	0.88 (0.97)	-	-
2009	-	-	-	-
2010	0.93 (0.05)	0.84 (0.07)	0.96 (7.49)	-
2011	0.90 (0.05)	0.90 (0.05)	0.91 (0.05)	-
2012	0.73 (0.09)	0.74 (0.08)	0.75 (1.60)	-
2013	-	-	-	-

Table 12. Survival rate (SEM) of white-footed mice between sampling occasions in no barberry in Storrs, CT.

Year	1	2	3	4
2007	0.90 (0.74)	0.92 (0.05)	0.72 (0.11)	0.88 (6.15)
2008	0.71 (0.14)	0.58 (0.88)	-	-
2009	-	-	-	-
2010	0.94 (0.05)	0.84 (0.07)	0.96 (7.40)	-
2011	0.90 (0.05)	0.90 (0.05)	0.91 (0.05)	-
2012	0.73 (0.10)	0.74 (0.09)	0.75 (1.60)	-
2013	-	-	-	-

Table 13. Japanese barberry cover (%) for study site in Redding, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	3	64	5
2008	0	61	5
2009	4	62	5
2010	1	66	5
2011	3	68	5
2012	2	72	3
2013	7	78	5

Table 14. Japanese barberry cover (%) for study site in North Branford, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	7	45	1
2008	0	46	1
2009	3	74	2
2010	15	51	1
2011	13	49	1
2012	28	51	2
2013	20	40	2

Table 15. Japanese barberry cover (%) for study site in Storrs, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	0	24	2
2008	0	26	1
2009	0	15	0
2010	0	29	1
2011	0	22	0
2012	0	20	0
2013	0	29	0

Table 16. Blacklegged ticks per hectare in Redding, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	516	934	67
2008	158	875	49
2009	217	524	17
2010	193	581	32
2011	225	1391	49
2012	220	620	0
2013	230	754	32

Table 17. Blacklegged ticks per hectare in North Branford, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	418	1233	166
2008	193	867	208
2009	292	383	109
2010	195	316	44
2011	783	1574	566
2012	519	689	69
2013	371	793	175

Table 18. Blacklegged ticks per hectare in Storrs, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	67	183	32
2008	74	126	17
2009	171	215	136
2010	10	67	17
2011	136	272	136
2012	30	59	49
2013	77	148	69

Table 19. Percent (%) infection *B.burgdorferi* in blacklegged ticks in Redding, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	35	50	0
2008	60	65	50
2009	65	49	100
2010	63	67	80
2011	68	64	60
2012	50	45	-
2013	17	46	0

Table 20. Percent (%) infection of *B.burgdorferi* in blacklegged ticks in North Branford, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	50	44	0
2008	45	71	43
2009	29	63	25
2010	72	43	71
2011	64	64	64
2012	72	56	71
2013	33	38	0

Table 21. Percent (%) infection of *B.burgdorferi* in blacklegged tick in Storrs, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	50	38	50
2008	50	50	-
2009	47	47	17
2010	0	50	33
2011	53	55	32
2012	0	17	33
2013	0	50	0

Table 22. Infected ticks per acre in Redding, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	74	189	0
2008	38	231	10
2009	57	104	7
2010	49	157	10
2011	62	360	12
2012	45	113	0
2013	16	141	0

Table 23. Infected ticks per acre in North Branford, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	84	222	0
2008	35	251	37
2009	34	98	11
2010	57	55	13
2011	203	408	147
2012	151	157	20
2013	50	122	0

Table 24. Infected ticks per acre in Storrs, CT.

Year	Managed Barberry	Full Barberry	No Barberry
2007	13	28	7
2008	15	25	0
2009	32	41	9
2010	0	13	2
2011	29	60	17
2012	0	4	7
2013	0	30	0

APPENDIX A
Mouse Population Statistics

ANOVA Mouse Population Estimate by Treatment

Categorical values encountered during processing are:
TREAT$ (3 levels) Control, Full, No

Dep Var: MOUSES   N: 40   Multiple R: 0.034   Squared multiple R: 0.001

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
TREAT$	26.102	2	13.051	0.022	0.979
Error	22351.482	37	604.094		

Durbin-Watson D Statistic   1.909
First Order Autocorrelation   0.033

ANOVA Mouse Population Estimate by Year

Categorical values encountered during processing are:
YEAR (5 levels) 2007,   2008,   2010,   2011,   2012

Dep Var: MOUSES   N: 40   Multiple R: 0.297   Squared multiple R: 0.088

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
YEAR	1968.257	4	492.064	0.844	0.507
Error	20409.327	35	583.124		

Durbin-Watson D Statistic   1.858
First Order Autocorrelation   0.047

ANOVA Mouse Population Estimate by Location

Categorical values encountered during processing are:

LOC$ (3 levels)   Egypt, Tommy, Uconn

Dep Var: MOUSES   N: 40   Multiple R: 0.419   Squared multiple R: 0.176

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
LOC$	3936.579	2	1968.289	3.949	0.028
Error	18441.005	37	498.406		

Durbin-Watson D Statistic   2.242

First Order Autocorrelation -0.139

COL/

ROW LOC$

  1 Egypt

  2 Tommy

  3 Uconn

Using least squares means.

Post Hoc test of MOUSES

Using model MSE of 498.406 with 37 df.

Matrix of pairwise mean differences:

	1	2	3
1	0.0		
2	-6.670	0.0	
3	-23.501	-16.830	0.0

Tukey HSD Multiple Comparisons.

Matrix of pairwise comparison probabilities:

	1	2	3
1	1.000		
2	0.741	1.000	
3	0.031	0.119	1.000

ANOVA Mouse Survival by Location

Categorical values encountered during processing are:
LOC$ (3 levels)
  Egypt, Tommy, Uconn

Dep Var: SURVIVAL   N: 129   Multiple R: 0.157   Squared multiple R: 0.025

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
LOC$	0.019	2	0.009	1.591	0.208
Error	0.747	126	0.006		

*** WARNING ***
Case   102 is an outlier   (Studentized Residual =   -3.770)

Durbin-Watson D Statistic   1.313
First Order Autocorrelation   0.333

ANOVA Mouse Survival by Year

Categorical values encountered during processing are:
YEAR (5 levels)
   2007,   2008,   2010,   2011,   2012

Dep Var: SURVIVAL N: 129 Multiple R: 0.225 Squared multiple R: 0.051

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
YEAR	0.039	4	0.010	1.649	0.166
Error	0.728	124	0.006		

*** WARNING ***
Case   102 is an outlier   (Studentized Residual =   -3.619)

Durbin-Watson D Statistic   1.332
First Order Autocorrelation 0.326

ANOVA Mouse Survival by Treatment

Categorical values encountered during processing are:
TREAT$ (3 levels)
  Control, Full, No

Dep Var: SURVIVAL   N: 129   Multiple R: 0.181   Squared multiple R: 0.033

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
TREAT$	0.025	2	0.013	2.140	0.122
Error	0.741	126	0.006		

Durbin-Watson D Statistic   1.315
First Order Autocorrelation   0.333

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