SOCIAL STRUCTURING OF A CENTRAL APPALACHIAN DEER HERD AND A TEST OF LOCALIZED MANAGEMENT

by

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(Under the Direction of Karl V. Miller)

ABSTRACT

Localized management has been proposed as a means of using white-tailed deer (*Odocoileus virginianus*) social behaviors in management. The process involves the "surgical" removal of a social group(s) of deer to create an area of low deer density for ≥5 years. However, this technique has only been tested in a highly philopatric, low-density, and un-hunted deer herd in New York. I conducted an experimental localized removal in a high-density deer population in the central Appalachians of West Virginia from 7 January to 27 February 2002. A total of 51 deer was removed within a 1.1 km^2 area, encompassing 2 forest regeneration sites. Herbivory data were collected during the summers of 2001–2004 from forest regeneration sites. Herbivory rates declined annually in both the removal and control areas, likely due to increased timber harvesting on the larger study site, suggesting that increasing forage availability may be a viable alternative management technique for mitigating impacts of overabundant deer populations. To evaluate spatial genetic structure, I performed a spatial autocorrelation analyses based on pair-wise Moran's I values among 229 individual adult (≥1.5 yrs.) females. Results revealed that genetic relatedness was related inversely to the distances between core areas determined by telemetry data or trapping location. Additionally, 28 social groups delineated by visual observation had a mean relatedness value within groups of 0.1, which is a value similar to that of first cousins. This evidence of fine-scale social group structuring indicates that the theoretical basis of localized management applies on the study site. However, the application of localized management only provided a temporary reduction in deer densities despite fulfilling *a priori* socio-behavioral requirements. During 1 January to 21 February 2005 I removed an additional 31 deer from the original removal area. Genetic analysis of deer collected in the second removal (i.e., repopulating animals) indicated they were different genetically from animals collected during the initial removal effort, suggesting that social behaviors of adjacent females may not prevent repopulation of removal areas by surrounding animals. The large number of repopulating animals and genetic evidence of population differentiation indicates that localized management may only produce temporary effects in Appalachian, high-density deer herds.

INDEX WORDS: Appalachians, forest regeneration, genetics, herbivory, localized management, microsatellites, *Odocoileus virginianus*, relatedness, rose-petal hypothesis, social groups, West Virginia, white-tailed deer

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INTRODUCTION AND LITERATURE REVIEW

Introduction

The recovery of white-tailed deer (*Odocoileus virginianus*) populations in the eastern United States from near extinction is one of the most significant success stories in wildlife conservation. However, abundant habitat and the absence of large predators in much of the today's deer range have resulted in elevated deer populations above historic levels in many areas. Because locallyoverabundant deer populations can negatively affect ecological processes and increase deer-human conflicts, resource managers must be able to effectively control deer populations.

Although regulated hunting controls deer populations in many areas, numerous examples of locally or regionally overabundant deer populations indicate that traditional management strategies are not always effective. Additionally, hunting is typically not an acceptable management option in some areas such as public parks or urban areas. As a result, biologists and forest managers must explore novel approaches for reducing negative ecological impacts of overabundant deer populations occurring at scales disparate from administrative application (e.g., county-level).

Recently an alterative management approach utilizing deer social behavior has been offered as a possible solution to locally overabundant deer populations. Although the single application of this technique was reportedly successful, its universal applicability in other areas has not been established. This study is an evaluation of this nontraditional management strategy at a study area in the central Appalachians, which was representative of many overabundant deer populations in the eastern United States.

Literature Review

Effects of deer overabundance

Overabundant deer populations can create highly conspicuous problems such as deer-vehicle collisions, depredation of agricultural crops, and damage to ornamental plantings (Conover 1997). The monetary estimates of these negative impacts were estimated by Conover (1997) at greater than $2 billion. Although some effects of overabundant deer populations are obvious, Waller and Alverson (1997) reported that changes to ecosystem processes may develop slowly and be subtle in appearance. Alteration of ecosystem processes certainly has biological costs and consequences; however monetary estimates are unknown.

White-tailed deer are considered a “keystone herbivore” because of their numerous direct and indirect effects on other species (Rooney 2001). Excessive herbivory is the primary mechanism responsible, although the effects of rubbing trees, trampling, defecation, and urination also can be severe (Danell et al. 2003). Augustine and Frelich (1998) noted that overabundant deer populations limited the reproduction and population structure of *Trillium* plants. The authors additionally speculated that local extirpation of preferred forbs was possible thereby reducing overall biodiversity. The future abundance of preferred species may also be reduced even after reduction of deer densities (Webster et al. 2005). Morphological changes of understory forbs have also been reported with increasing herbivory rates (Anderson 1994).

Structural changes to forest understories from white-tailed deer herbivory can impact numerous animal species. A 9 year study in northern Virginia by McShea and Rappole (2000) comparing songbird abundance and vegetation composition between fenced and unfenced sites determined that high deer densities can reduce populations of ground and intermediate canopy bird species by reducing the density and diversity of understory vegetation. Using simulated deer densities ranging from 3.7–24.9 deer/km^2, deCalesta (1994) noted that intermediate canopy-nesting songbird species richness and abundance declined 27% and 37% respectively, between the lowest and highest deer densities. Additionally, small mammal communities can be altered by white-tailed deer herbivory (Brooks and Healy 1988).

Numerous studies conducted on the Allegheny Plateau in Pennsylvania documented the problems of excessive herbivory in regenerating forests. Marquis (1974) observed that regeneration failures occurred in 25–40% of the areas examined due to deer herbivory. Additionally, even where regeneration was successful in Allegheny hardwoods, species composition and rotation lengths were affected (Marquis 1981). Preferential browsing by white-tailed deer in Allegheny hardwoods can increase the proportion of black cherry (*Prunus serotina*) and striped maple (*Acer pensylvanicum*) regeneration, and reduce abundance of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), and birch (*Betula* spp.) (Tilghman 1989).

Less palatable or preferred herbaceous vegetation that competes with woody regeneration may increase in regeneration areas in the presence of moderate to heavy herbivory rates. In a statewide survey of forest regeneration in Pennsylvania, McWilliams et al. (1995) found levels of fern and grass able to retard tree-seedling development at 54% of sample sites. A correlation between deer density and percent fern cover has been reported (Tilghman 1989). Additionally, Trumbull et al. (1989) noted in a comparison of fenced and unfenced 13 year old regeneration areas on the Allegheny Plateau in Pennsylvania, that grass and sedge cover was higher in unfenced areas.

Although the number of published investigations of herbivory impacts on central Appalachian forests is limited, areas with elevated deer densities would likely be impacted similarly to areas on the Allegheny Plateau in Pennsylvania. An examination of an industrial forest in the central Appalachians by Campbell et al. (2006) indicated that without management activities to reduce herbivory, many parts of the region would face regeneration problems. The estimated deer density on the study site was 12–20 deer/km^2 (Langdon 2001), which exceeds the ≤7 deer/km^2 level recommended for northern hardwoods by Tilghman (1989). Successful woody regeneration has been reported in southern Appalachian areas with deer densities of 6–8 deer/km^2 (Ford et al. 1993). A study by Collins and Carson (2002) on the same site as Campbell et al. (2006) indicated that herbivory by deer changed the succession process and masked any beneficial effects of fire or light availability for establishment of northern red oak seedlings (*Quercus rubra*).

White-tailed deer social structure

White-tailed deer social groups are typically composed of either female groups composed of adult does and their offspring, or male groups composed of adult and yearling males (Marchinton and Hirth 1984). Male and female social groups do not usually associate during the non-breeding season (McCullough et al. 1989). However large mixed-sex groups are common during winter after the breeding season (Lingle 2003), although such associations are temporary because groups do not travel and bed together as a single unit (Hawkins and Klimstra 1970).

Membership within groups is more fluid for bucks than does (Demarais et al. 2000). Additionally, buck social groups do not persist during the breeding season; instead males isolate themselves from other males during this period (Hawkins and Klimstra 1970). Interactions between males and female social groups are common during the breeding season as males investigate females approaching estrus (Marchinton and Hirth 1984).

Female social group membership is stable with the exception of the fawning season (Hawkins and Klimstra 1970). During the fawning season females isolate themselves approximately 2 weeks prior to and 4 weeks after parturition (Ozoga et al. 1982). During this period, female offspring from the previous summer (now yearlings) do not associate with their dams and may attempt to temporarily join male social groups (Marchinton and Hirth 1984). However Hawkins and Klimstra (1970) noted that 90% of yearling females without fawns of their own rejoined their mothers by early fall.

Social status within groups is a simple dominance hierarchy determined by age, size, and sex (Townsend and Bailey 1981). Within female social groups, dominance status is typically a function of age (Hirth 1977). Although male social dominance is influenced by age, research with captive deer indicates that dominance ranks are not always stable throughout the breeding season (DeYoung et al. 2006). Additionally, the oldest male in a group may not be the most dominant individual (Miller et al. 1987). Social dominance not only increases access to potential mates, it may increase the chance of survival during periods of food scarcity (Robinson 1962).

Dispersal from natal areas has been reported for both male and female white-tailed deer although dispersal rates are much higher in males (Miller and Marchinton 1995). The hypotheses for male dispersal have been speculated as either maternal aggression (Holzenbein and Marchinton 1992) or sexual competition (Shaw et al. 2006). Male dispersal rates may exceed 70% (Rosenberry et al. 2001, Campbell et al. 2005, Long et al. 2005), whereas female dispersal rates are low (2–20%; Hawkins and Klimstra 1970, Nelson 1993), however high female dispersal rates (>40%) have been reported in fragmented agricultural areas (Nixon et al. 1991).

Spatial genetic structure of white-tailed deer

Several studies have investigated macrogeographic spatial genetic structuring of white-tailed deer. Evaluations of the effects of restocking efforts on genetic variability across deer populations in western Tennessee (Kollars et al. 2004) and Mississippi (DeYoung et al. 2003) concluded that past restocking efforts contributed to spatial genetic variation. An examination by Purdue et al. (2000) of 6 deer populations from the Coastal Plain in Georgia and South Carolina found significant differentiation among populations based on maternally inherited mitochondrial DNA. Based on 4,749 individuals typed at a single allozyme marker with 3 alleles, Scribner et al. (1997) found evidence for spatial genetic structuring for a deer population in the Upper Coastal Plain of South Carolina. However the diameters of the "spatial clusters" were several kilometers. Few studies have examined microgeographic spatial genetic structure (<1 km) in white-tailed deer.

White-tailed deer may be expected to have minimal microgeographic spatial genetic structure because of their potential for long-distance dispersal (Scribner et al. 1997, Purdue et al. 2000). Dispersal of juvenile males is common (Rosenberry et al. 2001, Campbell et al. 2005), and dispersal distances range from a few kilometers in heavily forested areas to dozens of kilometers in open habitats (Long et al. 2005). Additionally, elevated rates of female dispersal have been reported in some populations (Nixon et al. 1991). Yet despite these confounding factors to gene flow restriction, evidence of microgeographic spatial genetic structure exists in some white-tailed deer populations.

Using radio-telemetry data from summer and winter ranges, Mathews and Porter (1993) identified putative female social groups in an unhunted, low density deer population in the Adirondack Mountains of New York. They reported that based on allozyme characteristics, genetic structure was present within social groups. The underlying mechanism responsible was assumed to be female philopatry that allowed formation of matriarchal social groups. However, they found no evidence for an association between genetic relatedness and spatial distance among social groups on summer ranges, only on separate winter ranges. They reported that the overlap of social groups on breeding ranges masked the expected negative relationship between genetic relatedness and spatial distance.

In contrast, Comer et al. (2005) found only limited evidence for microgeographic spatial genetic structuring for the same study site as Scribner et al. in South Carolina (1997). A history of intensive harvests reduced the age structure among does and may have elevated the dispersal rate of young female deer on their study site. They concluded that microgeographic social structuring may not exist in exploited deer populations where the formation of persistent cohesive social groups is limited.

Alternative management: Localized Management

A wide variety of alternative management techniques for controlling deer populations have been tested, however results have been mixed. Translocation often is proposed as a viable non-lethal technique for reducing urban deer populations. However an evaluation of the efficacy of translocation conducted by Beringer et al. (2002) found that annual survival rates of translocated animals were 0.30, compared to 0.69 for radio-collared resident deer in the release area. Additionally, costs averaged $387 per translocated deer for that study, and translocation was considered more costly than alternative methods. Fertility control also has been suggested as a non-lethal technique for reducing deer populations. However fertility control may be unsuitable for application on large areas (Rudolph et al. 2000), and can require a substantial amount of time before reductions in population densities occur (Merrill et al. 2006). Applications of lethal measures such as sharpshooting may be viewed unfavorably by the public (Messmer et al. 1997); however, sharpshooting has been shown to be safe and effective (Doerr et al. 2001).

Localized management is an alternative management technique that proposes removing a social group(s) to create a persistent (10–15 years) small-scale area (<2 km^2) of reduced deer density (Porter et al. 1991). Application sites for localized management would include areas where traditional population control (i.e., sport hunting) is ineffective or inappropriate. Specifically, parks and suburban areas appear to be well-suited for localized management (Porter et al. 1991, Kilpatrick et al. 2001, Porter et al. 2004). Forest regeneration sites located in remote areas where access to the hunting public is difficult or problematic also may benefit from an application of localized management prior to timber harvesting to ensure successful regeneration (Campbell et al. 2004).

The localized management concept is based on a 30-year series of studies conducted on a population of white-tailed deer in the Adirondack Mountains of New York. An examination of seasonal movements and home ranges of 105 radio-collared and 266 individually marked deer identified 9 social groups and determined that range fidelity and group membership was unchanged across years (Tierson et al. 1985). It was assumed that social groups were composed of related females and male offspring of pre-dispersal age. Additionally, Tierson et al. (1985) noted that female offspring formed home ranges adjacent to and usually overlapping the female parent.

Based on the sociobiological characteristics of the deer population in the New York site, Mathews (1989) determined that female social groups are structured as a series of overlapping home ranges. Older females produce philopatric female offspring whose home ranges partially overlap the home range of the central matriarch while radiating outward. The theoretical shape of these ranges is similar to the petals of a rose, and has been termed the “rose-petal hypothesis”. Thus population expansion occurs slowly as new females are added to the periphery of existing social group home ranges.

Utilizing the social behaviors suggested by the rose-petal hypothesis, localized management proposes that when a social group is removed, the site fidelity of adjacent social groups should prevent rapid recolonization. This theory of population expansion contrasts the “gas diffusion” model where no social structure is present, and deer move from high-density areas to low density areas (Porter et al. 1991). The persistence of created voids is determined by female fawn production, juvenile female dispersal rates, the probability a dispersal occupies the void, and the site fidelity of adjacent social groups.

McNulty et al. (1997) conducted an experimental test of the localized management technique on the New York study site by. A total of 14 females was removed from a targeted social group containing 17 deer. They created a 1.4 km^2 low-density area (retrospectively calculated), and no adjacent female deer (n=9) recolonized the area during 2 years of monitoring. A subsequent examination of the removal area by Oyer and Porter (2004) reported continued reduced deer densities for a period of 5 years.

Miller (1997) cautioned that the behavioral plasticity of white-tailed deer may limit the universal applicability of behavior based management techniques. The central requirement of localized management is the philopatry of juvenile females (McNulty et al. 1997). High rates of female dispersal (>40%) have been reported in fragmented agricultural areas of the Midwest (Nixon et al. 1991). Additionally, Comer et al. (2005) speculated that areas with heavy annual harvests and young age structure among does also may have higher dispersal rates. Therefore, population management recommendations based on the demographics of one population may not be applicable in all areas.

Objectives and Guide to the Dissertation

My research is the culmination of research investigating white-tailed deer and forest ecology on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia. This research was initiated by Drs. Tyler A. Campbell and Benjamin R. Laseter who investigated the movement ecology (Campbell 2003), and spatial and genetic structure of the deer population (Laseter 2004). Building on the foundation of their research initiated in 1999, the objectives of my dissertation are to examine the effects of deer herbivory on forest regeneration, explore alternative techniques to mitigate deer herbivory, and improve the understanding of white-tailed deer spatial, genetic, and sociobiological characteristics.

My dissertation is organized as a series of manuscript-style chapters addressing the objectives of this study. Chapter 1 is a review of literature relevant to the various aspects of this study. It covers the impacts of deer overabundance, the current understanding of white-tailed deer social structure, the relationship between spatial location and genetic structure in deer populations, and an alternate management strategy for controlling overabundant deer populations. Chapter 2 is a report on the impacts of deer herbivory on regenerating forests in the central Appalachians, and an assessment of the relationship between silvicultural practices and herbivory rates. Chapter 3 is an investigation of the relationship between spatial location and genetic relatedness of individual adult female deer. Additionally it evaluates the relatedness of members among adult females within social groups delineated by visual observations, and examines their spatial location and relatedness among social groups. Chapter 4 presents the results of the application of localized management and its effectiveness for prevention of forest regeneration failures. Chapter 5 is a comparison of the genetic relatedness of deer removed during the application of localized management with animals collected 3 years later from the same removal area (i.e., repopulating animals). Chapter 6 is a summary of the findings for all of the manuscript chapters. Manuscripts based on chapters 2–5 will be submitted to *Forest Ecology and Management* (chapter 2), the *Journal of Mammalogy* (chapter 3), and the *Journal of Wildlife Management* (chapters 4 and 5).

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CHAPTER 2

DEER HERBIVORY AND TIMBER HARVESTING RATES: IMPLICATIONS FOR REGERATION SUCCESS[1]

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[1] Miller, B. F., T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. To be submitted to *Forest Ecology and Management*.

Abstract

Herbivory by white-tailed deer (*Odocoileus virginianus*) can greatly affect forest regeneration. Typical measures to ensure forest regeneration have included physical barriers or direct manipulation of deer densities. However altering silvicultural practices to provide abundant deer forage has not been tested thoroughly. We examined browse species preferences, changes in herbivory rates, and species establishment in 1–6 year old regeneration areas from 2001–2004 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia. Our results indicate that woody vegetation grown in full sunlight reached the maximum plot coverage by the fourth growing season and was unaffected by competing herbaceous vegetation. However the establishment of less abundant woody species, such as northern red oak (*Quercus rubra*), may be inhibited when browsed greater than or proportionally to occurrence. Based on relative use, relative abundance, and browse preferences data, we predict that future forests on our study area will be composed of American beech (*Fagus grandifolia*), birch (*Betula* spp.), maples (*Acer* spp.), and yellow-poplar (*Liriodendron tulipifera*). Herbivory rates declined precipitously as the amount of early successional habitat increased on our study site. We conclude that providing approximately 14% of an area in well-distributed, even-aged managed forests can have substantial impacts on reducing herbivory rates. However, silvicultural practices should consider effects on hard mast production, habitat requirements of other species, and hardwood lumber marketability.

Keywords: Allegheny hardwood-northern hardwood; browse preferences; herbivory; *Odocoileus virginianus*; regeneration; timber harvesting; West Virginia; white-tailed deer

Introduction

The recovery of white-tailed deer (*Odocoileus virginianus*) populations in the eastern United States from near extinction is one of the most significant success stories for wildlife conservation (McCabe and McCabe, 1984). Although hunting is used to control deer populations in most instances, coarsely managing populations at the county level or greater can lead to overabundant deer populations in localized areas (McShea and Rappole, 2000; Waller and Alverson, 1997). As a result, biologists and forest managers are challenged by the effects of overabundant deer on ecological communities at scales disparate from administrative application.

White-tailed deer primarily alter ecosystem processes by excessive herbivory, although the effect of rubbing trees, trampling, defecation, and urination also can be severe (Danell et al., 2003). Overabundant deer populations may reduce the current abundance and morphology of herbaceous plant species (Augustine and Frelich, 1998; Anderson, 1994) and affect future abundance of browse sensitive species even after reduction of deer densities (Webster et al., 2005). Additionally, changes to forest understories from excessive herbivory can alter abundance and diversity of songbird (McShea and Rappole, 2000; deCalesta, 1994) and small mammal communities (Brooks and Healy, 1988).

The effects of excessive herbivory are especially problematic for regenerating forests because long-term successional patterns may be altered (McWilliams et al., 1995; Trumbull et al., 1989; Alverson et al., 1988; Horsley and Marquis, 1983; Marquis, 1981). These impacts can include shifts in woody and herbaceous species composition, reduced stocking, extended rotation lengths, and perhaps entire regeneration failures (Horsley et al., 2003; Tilghman, 1989; Marquis, 1974).

Measures to reduce herbivory by white-tailed deer to ensure regeneration success have involved either manipulating deer densities (Behrend et al., 1970; McNulty et al., 1997), installing deer-proof fencing (Brenneman, 1982), or providing abundant summer forage by concentrating silvicultural activities to alleviate browsing pressure within intact forests and regeneration areas (Stout and Lawrence, 1996; Stout et. al., 1996, 1993; Marquis et al., 1992; Tilghman and Marquis, 1989). However the interspersion of timber harvests across an area, and proportion of the area composed of timber harvests necessary to effectively reduce deer herbivory have not been identified. To date, no scientific studies have empirically documented the timber harvest regime necessary to mitigate excessive herbivory by white-tailed deer.

A preliminary analysis on our study site investigating the effects of spatial and physical factors on herbivory pressure determined that forest regeneration and forest health were at risk from excessive herbivory (Campbell et al., 2006). In this study, we investigated the impacts of deer herbivory on regenerating forests in the central Appalachians. We also assessed the relationship between timber harvests and herbivory rates toward developing forest management guidelines to reduce the impacts of herbivory on regenerating and unharvested forests.

Study area

Our study was conducted on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) in southwestern Randolph County, West Virginia. The MWWERF was established by Westvaco Corp. in 1994 to examine the impacts of modern industrial forestry on the landscape and its ecological processes in a Central Appalachian environment (Keyser and Ford, 2005). The 3,413-ha MWWERF is located in the Unglaciated Allegheny Mountain and Plateau physiographic province (38°42’N and 80°3’W). Landscape features consist of broad, plateau-like ridgetops with steep sides and narrow valleys with small, high-gradient streams. Elevations range from 700 to 1,200 m. The climate is moist and cool with mean annual precipitation in excess of 155 cm (Strausbaugh and Core, 1977). Soils of the MWWERF are acidic, well-drained Inceptisols (Schuler et al., 2002).

Forests on the MWWERF are naturally regenerated, second-growth stands established in the early 1900's following extensive area-wide railroad logging (Clarkston, 1993) or younger stands resulting from harvests of those second-growth forests over the past 20 years. Currently the forests are managed primarily by even-aged harvesting with an 80-100 year rotation length (Adams, 2005). Harvest areas are well distributed throughout the MWWERF with an average size of 15 ha. Timber harvests implemented in the early 1990's failed to regenerate successfully because of excessive herbivory.

The most common forest type is Allegheny hardwood-northern hardwood forests composed of American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), black cherry (*Prunus serotina*), and Fraser magnolia (*Magnolia fraseri*). Cove hardwoods and mixed-mesophytic forests composed of yellow-poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*), sweet birch (*Betula lenta*), and northern red oak (*Quercus rubra*) are common at elevations less than 850 m. Elevations over 1,000 m and sheltered riparian areas contain significant amounts of eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*). A shrub layer and understory groundcover is absent in many areas with the exception of rhododendron (*Rhododendron maximum*) thickets in higher upland areas and riparian areas, and thick mats of hay-scented fern (*Dennstaedtia punctilobula*) in areas where the canopy is interrupted.

Intensive research of the deer population on the MWWERF began in 1999 (Campbell, 2003). Population densities on the MWWERF were estimated as 12-20 deer/km^2 at the beginning of our study (Langdon, 2001). Based upon visual observations recorded throughout the study, deer densities remained constant (B. Miller, unpublished data). The hunting public was allowed access to the MWWERF, however access to the area by vehicle was restricted. Bucks on the MWWERF experience high annual mortality from hunting, whereas females average approximately 85-90% annual survival (Campbell et al., 2005). Abomasal parasite counts indicated that the deer population was at or near nutritional carrying capacity (Fisher, 1996).

Methods

Study design

Beginning in 2001, we collected vegetation and browse data from 8, 1-3 year old regeneration sites ranging from 8 to 19 ha in size (Campbell et al., 2006). All regeneration sites were then resampled in 2002 and 2003. In 2004, 4 of the 8 regeneration sites were omitted from additional sampling as most woody browse exceeded herbivory height. During the study period we collected a total of 28 observation-years from regeneration sites ranging in age from 1-6 years old.

Within each regeneration site, we established 90 1-m^2 permanent sampling plots. Thirty plots were distributed systematically along the edge of skidder trails at intervals of approximately 120 m. We installed 30 additional plots matched to the plots along skidder trails, but located 5 m into the regeneration area perpendicular to the skidder trail. Additionally, we established 30 plots in the adjacent unharvested mature forests ≥ 50 m from the edges of regeneration sites, and distributed systematically in transects parallel to regeneration sites. The mean distance between mature forest plots was 19 m.

We sampled all plots between 15 July and 15August of each study year. Within each year we sampled plots within ±7 days of their original sampling date in 2001 to prevent temporal bias resulting from potential changes in vegetation structure, species composition, or herbivory rates.

Plot coverage estimates

We recorded ocular estimates of plot coverage by ferns, forbs, grasses, woody vegetation, and non-vegetation (e.g., rocks, woody debris, litter, and bare ground) within each 1 m^2 plot (Higgins et al., 1994). We obtained coverage estimates from 1.5 m above each plot, totalling 100%. Mean and standard error plot coverage for each category were calculated for each growing season. Percentages were transformed by $\log_{10}(x)$ and tested for normality using the Shapiro-Wilk test statistic (SAS Institute, 2002). We performed one-way analysis of variance tests (ANOVA) on each coverage category to test for differences ($P<0.05$) among years (SAS Institute, 2002). If significant differences were detected, we used Tukey's honestly significant difference tests for multiple comparisons.

Herbivory data collection and analysis

Following Ford et al. (1993), we recorded the total number of browsable units (i.e., twig tips) available of semi-woody (e.g., *Rubus* spp.) and woody plants ≤1.5 m from the ground. The species of each browsable unit was recorded, and each unit was assigned to a browsed or unbrowsed category. All browsing was assumed to be caused by white-tailed deer because no herbivory by other vertebrates was identified. Only species averaging more than 4,000 browsable units/ha (>4 units/10 m^2) were included in our analyses.

We calculated percent of available twigs browsed (PATB), relative abundance (RA), and relative use (RU) for each species as follows: PATB = (number of units browsed for a species /

total number of units available for a species) * 100; RA = number of units available for a species / number of units available for all species) * 100; RU = number of units browsed for a species / number of units browsed for all species) * 100 (Strole and Anderson, 1992).

To assess preferences of deer for individual plant species, we summed the number of browsable units and the number browsed for each species across all plots within each regeneration area and sampling year. We performed a Z-test to determine whether the use of a species was greater than, proportional to, or used less than its proportion of the total number of browsable units available. This Z-test was performed on each species in each regeneration area to determine species preference across a range of sites and stand ages.

Scale and distribution of regeneration areas

We analyzed timber harvest records and stand locations for the MWWERF using MeadWestvaco's Forest Research Information System geographical databases. To determine the proportion of the study area <10 years of age, we summed the number of hectares harvested in the previous 10 years for each year and then divided by the total property area. To evaluate the impacts of forest management on browsing rates, we calculated a total browsing rate for each year for unharvested and regeneration areas. Total browsing rates (±SE) were calculated by averaging the mean browsing rates of all stands examined in a sampling year

We used Arcview GIS 3.3 (Environmental Systems Research Institute, 1999) to evaluate the spatial distribution of regeneration sites on the MWWERF. We created a series of buffers around regeneration sites <10 years of age (in 2004) with 100m distance intervals. The number of hectares within each distance interval was calculated in Arcview using the Xtools extension and divided by the total property area to determine what proportion of the study site was composed of each distance interval.

Results and discussion

Plot coverage estimates

Characteristics of regeneration sites changed across a successional gradient (Fig. 2.1). Coverage estimates of the non-vegetation category (e.g., rocks, woody debris, litter, and bare ground) differed significantly among stand ages ($F_{5,22} = 83.7$, $P < 0.001$). The non-vegetation category declined from 79% plot coverage during the first growing season to 41% plot coverage in the second growing season. Plot coverage estimates of the non-vegetation category did not differ among the third through the sixth growing seasons.

Plot coverage estimates of woody vegetation differed among stand ages ($F_{5,22} = 13.7$, $P < 0.001$), and increased with stand age. Plot coverage of the woody vegetation category was lowest in the first growing season (15%). Coverage of woody vegetation in the second and third growing season was 48% and 67% respectively, but did not differ statistically. The coverage estimates of both seasons were greater than estimates of woody vegetation in the first growing season. Woody vegetation coverage was greatest in the fourth growing season in which >74% of the plot was composed of woody vegetation. After the fourth growing season, some woody vegetation exceeded the 1.5 m sampling height, therefore subsequent plot coverage estimates of woody vegetation declined. As a result, plot coverage estimates of woody vegetation for the fifth and sixth growing season were less than the fourth growing season estimates, and did not differ from estimates of the second and third growing seasons.

Forb coverage was <1% in five of six growing seasons. The greatest coverage occurred during the second growing season (2.5%), however no differences ($F_{5,22} = 1.80$, $P = 0.15$) were detected among growing seasons. American pokeberry (*Phytolacca americana*) was the most commonly observed forb species. Pokeberry is a ruderal plant found on disturbed sites such as timber harvests or burned areas, and is commonly consumed by white-tailed deer (Johnson et al., 1995).

No differences were detected for the grass category among growing seasons ($F_{5,22}$ = 0.48, P = 0.79). Percent cover of grasses can be positively related to deer density, and the presence of grasses can compete with seedlings and reduce regeneration success (Horsley et al., 2003). However, mean plot coverage by grass was <4% for the six growing seasons examined and it had little impact on current regeneration success.

Fern coverage primarily consisted of hay-scented fern, with a small proportion (<10%) of Christmas fern (*Polystichum acrostichoides*). We detected no differences for the fern category among growing seasons ($F_{5,22}$ = 1.33, P = 0.29). Although not statistically significant, mean plot coverage estimates were highest for the fern category in the fifth and sixth growing seasons. The increases in the fifth and sixth growing seasons likely are due to the reduction of plot coverage by woody vegetation as woody species increased in height.

Woody and semi-woody species established rapidly on the regeneration areas despite the presence of competing herbaceous vegetation. Unless timber harvests provide large amount of available light, such as clearcuts, seedling growth may not be adequate to outpace the growth of competing vegetation (e.g., grasses and ferns) (McWilliams et al. 1995). Additionally, Fredrickson et al. (1998) reported a positive relationship between available light and the recruitment of seedlings. Our results are consistent with the positive relationship between light and vegetation performance, however it should be emphasized that some locations with extremely high deer densities or small acreage timber harvests may not adequately regenerate even in the presence of abundant light.

Species composition

We recorded browsable units from a total of 38 woody, and 4 semi-woody plant species. However, 12 species (Table 2.1) constituted 85% of the available browsable units (238,571 of 280,764) recorded in our study. Nine of the 12 most common species were overstory components prior to timber harvesting. Three early successional invaders including fire cherry (*Prunus pensylvanica*), striped maple (*Acer pensylvanicum*), and blackberry (*Rubus* spp.) also were common in regeneration areas.

Relative abundance values ranged from 0 to 48.9 across species and growing seasons (Table 2.1). The relative abundance of blackberry was highest across all growing seasons. Black cherry, fire cherry, red maple, and birch (primarily *B. lenta*) were the most common woody species during the first growing season. However, black cherry and fire cherry abundance decreased over time, whereas birch abundance increased. American beech was the ninth most abundant species during the first growing season, but increased to the third most abundant species by the sixth growing season. Northern red oak and witch-hazel (*Hamamelis virginiana*) were limited in abundance throughout the six growing seasons.

Browse preferences

The browse preferences we observed were in general agreement with those reported for other Allegheny and northern hardwood forests. The browsing rates for American beech, red maple, birch, sugar maple, black cherry, yellow-poplar, and striped maple were proportionally less than their occurrence in the population on the MWWERF for over 50% of the examined site-years (Fig. 2.2). American beech, black cherry, and striped maple are commonly considered non-preferred species that often increase in abundance or relative to other woody species in areas in response to high deer densities (Horsley et al., 2003; Tilghman, 1989). Previously reported browse preferences and responses to herbivory pressure are more variable for maples, birch, and yellow-poplar. Discrepancies of species use between our study and those previously reported may be attributed to effects of methodologies (Fredericksen et al., 1998), differences in species composition among sites (Gill, 1992), or non-linear responses to herbivory (Rooney and Waller, 2003).

The low browsing rates and increase in abundance of American beech and birch across the growing seasons suggests that at least in the short-term, these species will be a substantial component of the forest overstory. In addition, red maple and yellow-poplar may become canopy species based on their low proportional use and moderate abundance. Although striped maple will not become a substantial component of any future overstory, its low RU may allow it to persist in the under- and mid-story.

Fire cherry, witch-hazel, magnolia, and northern red oak were browsed in proportion to occurrence in >50% of sites examined (Fig. 2.2). Previous research on this study area by McGill et al. (2003) investigating the response of fire cherry to prescribed fire, partial canopy removal, and white-tailed deer herbivory found that the development of unfenced seedlings was reduced by deer herbivory. Our observed decline in RA over time supports their results and is likely reflective of the high PATB in the first three growing seasons.

Northern red oak and witch-hazel had low RA values across the growing seasons (Table 2.1). Herbivory impacts may be particularly important to species with lower availability. Because northern red oak is a commercially important species that is difficult to regenerate (Gribko et al., 2002; Buckley et al., 1998; Lorimer, 1993), the effects of herbivory are particularly important for this species. An investigation of the relationship between prescribed fire, canopy gaps, and deer herbivory on this study site by Collins and Carson (2002) indicated that herbivory by deer changed the succession process and masked any benefits of fire or increased light availability for establishment of northern red oak seedlings. The low RA value for northern red oak we observed across all growing seasons raises questions regarding its future as an important canopy species on the MWWERF.

Blackberry was browsed proportionally greater than its occurrence in >92% of sites examined (Fig. 2.2). Additionally blackberry had higher average PATB and RU values than all other species for all growing seasons (Table 2.1). The high preference by deer and availability of blackberry may enable it to act as a buffer species to reduce pressure on valuable hardwood species. Moser et al. (2006) reported that *Rubus* spp. protected tree saplings from heavy browsing by roe deer (*Capreolus capreolus*) by providing an attractive forage that reduced dependence on other species and reduced accessibility to other species. However, the presence of blackberry in regeneration sites is limited to the first few growing seasons (Harlow and Downing, 1970), and extensive levels of blackberry in the understory have been implicated in reducing seedling development in some hardwood stands (Bashant et al., 2005).

Timber harvests and browsing rates

Two past timber harvests implemented in 1993 and 1994 on the MWWERF failed to adequately regenerate as a result of excessive herbivory (P. Keyser, MeadWestvaco, personal communication). This occurred because o other even-aged timber management existed within a 4,000 ha matrix of forest at that time, therefore <0.5% of the property was in early successional habitat. Although no past estimates of deer densities are available, anecdotal accounts suggest moderate to high deer densities similar to densities observed by Langdon (2001).

The proportion of the study area composed of harvested areas <10 years old increased from approximately 8% to 14% during the duration of the study (Fig. 2.3). Overall timber harvest rates were approximately 2% per year during the course of this study, however harvesting rates of smaller (400–700 ha) regions within the property varied between 1–5% per year. Overall mean browsing rates for sample plots in regeneration sites and in unharvested areas declined precipitously as the amount of early successional habitat increased (Fig. 2.3).

Deer use of regeneration areas declines when regeneration becomes too dense, and/or when forage exceeds the reach of deer (Blymyer and Mosby, 1977). However our average stand age (±SE) for the final sampling year (2004) was only 5.0 ± 0.6 years of age. Additionally, the decreased browsing rates were observed in adjacent mature forest sites where palatability and vegetation density likely remained constant.

Instead, the increased proportion of early successional habitat may have greatly increased the ecological carrying capacity on the study area. In fact, increased harvesting intensity of forests has been suggested as a means to reduce overall browsing pressure and ensure regeneration success throughout the central and southern Appalachians (Kalen, 2005; Ford et al., 1993; Marquis et al., 1992; Tilghman and Marquis, 1989). Stout et al. (1993) reported that a combination of a 14% complete overstory removal, and a 33% partial cutting was effective for ensuring stand establishment on a 445- ha forested site in the Allegheny hardwood region of northern Pennsylvania. Our results confirm these suggestions but also demonstrate that the addition of partial cuts may not be necessary in all situations. According to our study, when approximately 14% of the area on our study site was composed of stand ages <10 years old, the browsing rates dropped to <5% for both regeneration areas and mature forests.

The distribution of regeneration areas also is an important determinant of browsing pressure. If harvests are concentrated in a specific area, herbivory rates in distant areas may not be affected. Marquis et al. (1992) suggested that the extent of timber harvesting within a 1,609-

m radius of a proposed harvest site will determine the impacts of deer herbivory. Augustine and Jordan (1998) found that the intensity of herbivory in forests was inversely related to the availability of agricultural fields within a 1,500-m radius.

By the final year of our study (2004), regeneration sites were well distributed across the MWWERF (Fig. 2.4). Based on our analysis, 86.5% of the area was within 500 m of a regeneration site. Previous investigations of summer home ranges of white-tailed deer on our study site by Campbell et al. (2004) determined that home range size of male and female deer were 101.2 and 81.5 ha, respectively. Assuming a circular home range, the respective radius for a male and female summer home range is 567 and 509 m. Therefore, despite only 14% of the MWWERF area comprised of harvested stands, abundant summer food resources were available to the majority of deer on our study site because of the spatial distribution of harvests.

Conclusions

Our results based on monitoring of the first six growing seasons indicated that natural regeneration grown in full sunlight was able to outgrow competing herbaceous vegetation. Our species preference analysis was similar to published reports. However our approach considered multiple temporal and spatial levels which incorporate differences in species composition and palatability. Blackberry forage was consistently the most preferred and available species in regeneration areas across all examined growing seasons. Its presence may act as a buffer to other species and reduce use of other woody species (Moser et al., 2006). Based on changes in relative abundance and relative use, we predict that future forests on the MWWERF will be composed of American beech, birch, maples, and yellow-poplar.

Since fencing or manipulation of deer densities with regulated hunting is not possible for some situations (Curtis et al., 1994; Warren, 1991), providing abundant browse by forest management is a viable option for reducing herbivory. Our results suggest that providing approximately 14% of an area in well-distributed, even-aged managed forests can have substantial impacts on herbivory rates. However applications of timber harvests should be implemented with consideration of hard mast retention, habitat requirements of other species, and hardwood lumber marketability.

Additional research is necessary to investigate the effects of increased forest harvesting on deer populations. Production of increased summer deer food resources may increase carrying capacity and stimulate deer population growth potentially exacerbating deer herbivory (Kramer et al., 2006; Ozoga and Verme, 1982). However, the removal of mature hardwoods reduces hard mast production and the associated effects on deer populations are not fully known. Therefore, applications of landscape level forest management must be coupled with sound deer management strategies.

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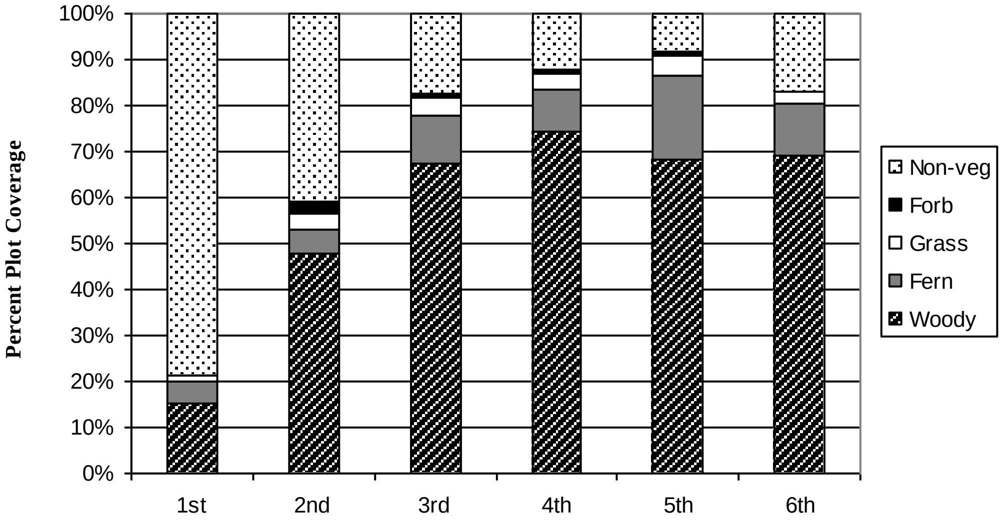

Fig. 2.1. Average percent of plot coverage by cover type and growing season. Data were collected from harvested sites in late summers of 2001-2004 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph county, West Virginia. Sample sizes by growing season were: 1st, n=3; 2nd, n=5, 3rd, n=8; 4th, n=7; 5th, n=3; 6th, n=2.

Table 2.1

The 12 most common woody and semi-woody browse species listed with their corresponding relative abundance (RA), relative use (RU), and percent browsed (PATB) by growing season on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph county, West Virginia. Data were collected from harvested sites in late summers of 2001-2004. Sample sizes by growing season were: 1st, n=3; 2nd, n=5, 3rd, n=8; 4th, n=7; 5th, n=3; 6th, n=2.

Species		1st	2nd	3rd	4th	5th	6th
Blackberries	RA	33.6	34.7	43.6	47.8	48.9	32.3
(*Rubus* spp.)	RU	64.9	59.4	68.4	84.6	90.7	86.3
	PATB	44.7	14.1	13.7	10.9	15.9	11.6
Black cherry	RA	19.2	17.5	7.5	4.7	2.7	3.6
(*Prunus serotina*)	RU	5.6	7.4	3.7	0.8	0.1	0
	PATB	6.7	3.5	4.3	1.1	0.3	0
Fire cherry	RA	13.2	14.8	3.9	3	0.7	0.9
(*Prunus pensylvanica*)	RU	11.6	16.4	6.9	1.3	0.3	0
	PATB	20.4	9.2	15.5	2.7	4	0
Red maple	RA	10.4	7.8	6	4.7	5.2	7.7
(*Acer rubrum*)	RU	2.8	3.8	1.5	1.7	0.5	1.8
	PATB	6.2	4.1	2.3	2.2	0.8	1
Birch	RA	6.1	8.3	12	19.2	16.7	22.5
(*Betula* spp.)	RU	4.3	6.1	8.2	5.5	4.1	5.1
	PATB	16.4	6.1	6	1.8	2.1	1
Magnolia	RA	5.2	2	1.5	1.7	3	4.9
(*Magnolia* spp.)	RU	4.2	1.2	1.9	0.8	0.1	2
	PATB	18.6	5	11.1	3.1	0.2	1.8
Striped Maple	RA	4.6	3.8	3.2	3.1	5	4.2
(*Acer pensylvanicum*)	RU	0	0.2	1.4	0.3	0.9	0.3
	PATB	0	0.4	3.9	0.5	1.5	0.3
Sugar Maple	RA	2.8	2.9	8.6	4.7	2.2	3
(*Acer saccharinum*)	RU	2.6	2	2.6	0.3	0.3	0.8
	PATB	21.4	5.6	2.6	0.4	1.3	1.1
American beech	RA	2	2.7	4.3	5.8	9.6	12.3
(*Fagus grandifolia*)	RU	2.8	1	0.5	0.3	0.4	0.8
	PATB	31.4	3.1	1	0.3	0.4	0.3
Yellow-poplar	RA	1.9	2.9	4.8	2.9	3.6	5.8
(*Liriodendron tulipifera*)	RU	0.7	0.9	1.7	1.7	1.4	2
	PATB	8.3	2.6	3	3.6	3.4	1.5
Witch-hazel	RA	0.9	1.9	1.8	1.4	0.8	1.1
(*Hamamelis virginiana*)	RU	0.5	0.8	2.5	1.9	0.1	0
	PATB	13	3.6	12	8.5	0.9	0
Northern red oak	RA	0	0.9	2.7	1.2	1.7	1.7
(*Quercus rubra*)	RU	0	0.6	0.8	0.7	1	1
	PATB	0	5.9	2.5	3.9	5.3	2.6

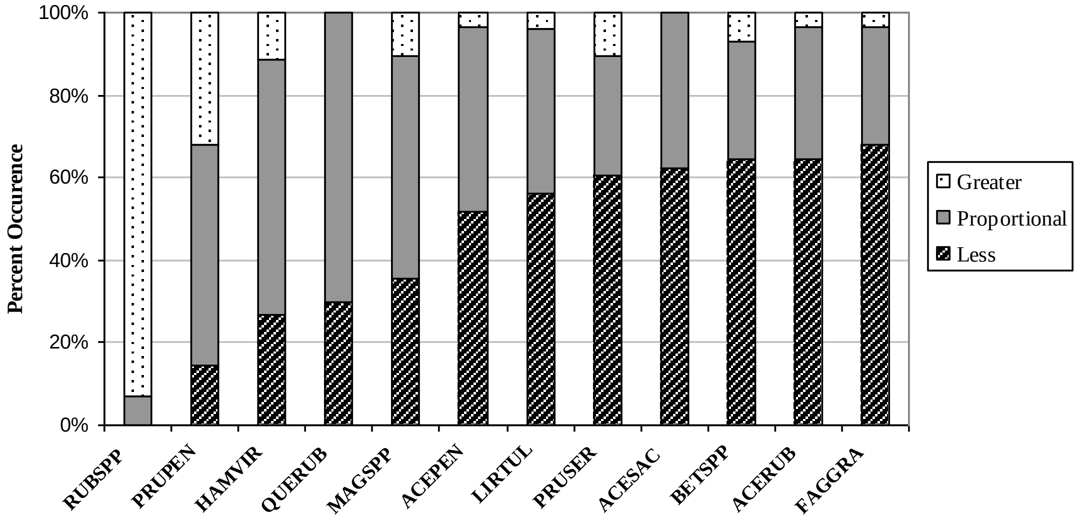

Fig. 2.2. Percent occurrence by usage category of the 12 most common woody and semi-woody browse species on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph county, West Virginia. Data was collected from harvested areas in late summer of 2001 (n=8), 2002 (n=8), 2003 (n=8), and 2004 (n=4) ranging in age from 1-6 years of growth. Species codes are as follows: RUBSPP, *Rubus* spp.; PRUPEN, *Prunus pensylvanica*; HAMVIR, *Hamamelis virginiana*; QUERUB, *Quercus rubra*; MAGSPP, *Magnolia* spp.; ACEPEN, *Acer pensylvanicum*; LIRTUL, *Liriodendron tulipifera*; PRUSER, *Prunus serotina*; ACESAC, *Acer saccharum*; BETSPP, *Betula* spp.; ACERUB, *Acer rubrum*; FAGGRA, *Fagus grandifolia*.

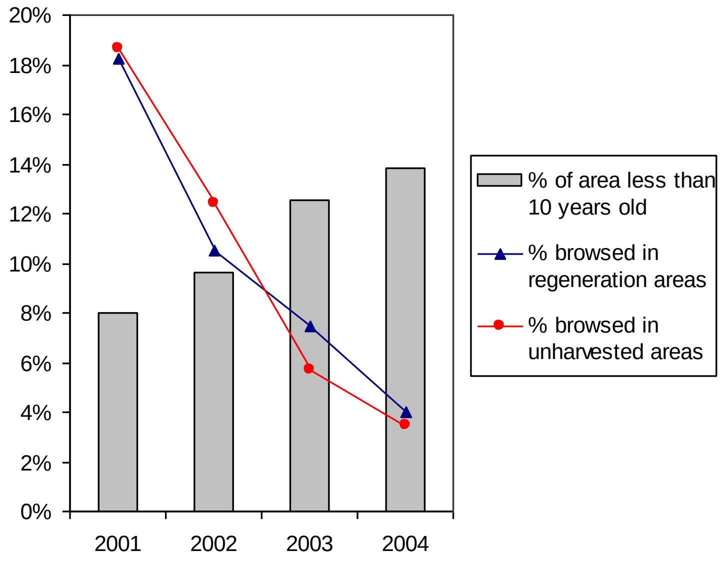

Fig. 2.3. Percentage of the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph county, West Virginia less than 10 years old and average percent browsed of regeneration areas and unharvested areas from 2001-2004. Regeneration site herbivory data were collected from harvested areas in late summer of 2001 (n=8), 2002 (n=8), 2003 (n=8), and 2004 (n=4) ranging in age from 1-6 years of growth. Unharvested area regeneration data were collected from sample sites adjacent to harvested areas.

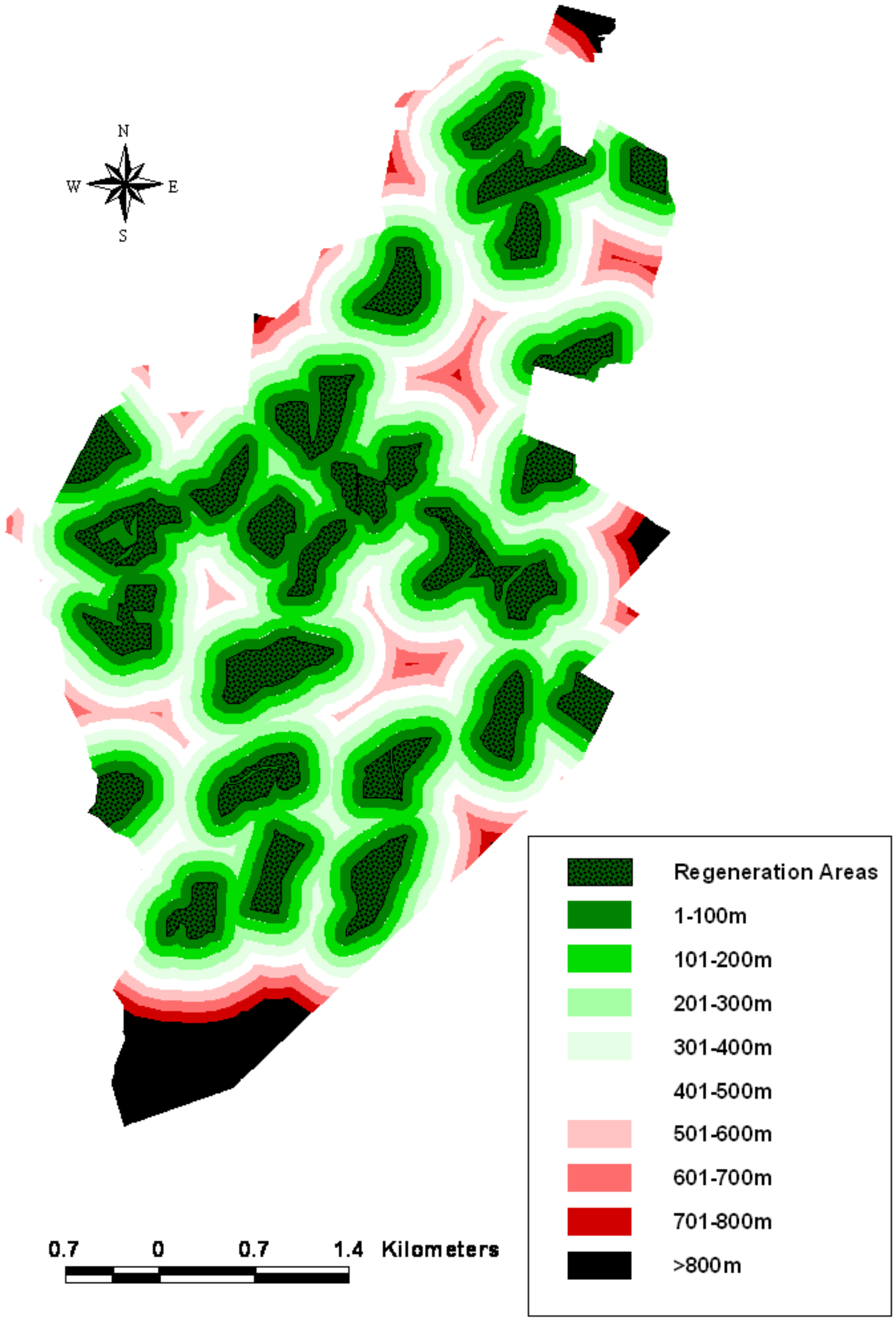

Fig. 2.4. Timber harvests (<10 years old) in 2004 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph county, West Virginia. Regeneration sites are buffered by 100 m distance intervals.

CHAPTER 3

MICROGEOGRAPHIC GENETIC AND SOCIAL STRUCTURING OF A CENTRAL APPALACHIAN DEER HERD[1]

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[1] Miller, B. F., R. W. DeYoung, T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. To be submitted to the *Journal of Mammalogy.*

Abstract- Although spatial genetic structure of white-tailed deer (*Odocoileus virginianus*) populations has been examined at coarse scales (>1km), most research has lacked the geographic and molecular resolution necessary to examine microgeographic patterns. We used 14 polymorphic microsatellite DNA loci to conduct a spatial autocorrelation analysis on 229 adult females from a 3,413 ha study area in the central Appalachians of West Virginia. Genetic relatedness was inversely related to geographic distances between individuals. Females with core areas separated by less than approximately 1,000 m were more related than randomly permuted values. Resulting correlograms displayed a stabilizing pattern, suggesting spatial structure at the group level. Using visual observations, we delineated 28 putative female social groups and found that the mean relatedness value within social groups was similar to that of first cousins. This suggests a causative mechanism of spatial fidelity of matrilineal social groups resulting from philopatric female offspring. Our evidence of microgeographic genetic and social structuring supports the basic premise of deer social dispersion.

Key words: genetics, microsatellites, *Odocoileus virginianus*, relatedness, social groups, spatial autocorrelation, white-tailed deer.

Introduction

Many ungulate species demonstrate spatial genetic structuring in contrast to the classical population genetics theory in which a population is composed of randomly mating individuals (Wright 1978). A wide variety of environmental and social factors can influence gene flow in ungulate populations. The effects of landscape features (Coulon et al. 2006; McLoughlin et al. 2004; Perez-Espona et al. 2006), isolation by distance (Balloux et al. 2002; Hardy and Vekemans

1999), and human influences (Blanchong et al. 2006) have been documented thoroughly. However the effects of social organization on gene flow have only recently been explored.

Although ungulate populations may be expected to have minimal spatial genetic structure due to their potential for long-distance dispersal (Scribner et al. 1997), spatial genetic structure attributed to social organization has been reported in red deer (*Cervus elaphus*—Frantz et al. 2008; Nussey et al. 2005), white-tailed deer (*Odocoileus virginianus*—Mathews and Porter 1993; Scribner et al. 1997), and Soay sheep (*Ovis aries*—Coltman et al. 2003). Typical social organization of ungulate populations consists of matriarchal social groups characterized by male-biased dispersal, high female philopatry, and polygynous breeding systems (DeYoung et al. 2002; van Hooft et al. 2003). These socio-behavioral attributes of ungulate social organization have the potential to create fine-scale spatial structuring in some populations (Storz 1999).

The social organization of white-tailed deer appears similar to that of other ungulates. In many areas of their distribution, white-tailed deer form matriarchal social groups containing adult females and several generations of offspring (Hawkins and Klimstra 1970; Hirth 1977; Mathews and Porter 1993). Additionally, previous research suggests that members of these social groups associate throughout the year (Aycrigg and Porter 1997; Nelson and Mech 1984). Although high female dispersal rates (>40%) have been reported in fragmented agricultural areas (Nixon et al. 1991), most female dispersal rates are low (2-20%; Hawkins and Klimstra 1970; Nelson 1993). Dispersal rates of juvenile males may exceed 70% (Campbell et al. 2005; Rosenberry et al. 2001) and dispersal distances range from a few kilometers in heavily forested areas to dozens of kilometers in open habitats (Long et al. 2005). Based on these socio-behavioral attributes, white-tailed deer are well suited for investigations of the effects of social organization on fine-scale spatial genetic structuring.

The preponderance of research investigating the spatial genetic structure of white-tailed deer populations has been examined at a macrogeographic scale (Blanchong et al. 2006; DeYoung et al. 2003a; Doerner et al. 2005; Kollars et al. 2004; Purdue et al 2000). Those few studies conducted at finer geographic scales (Mathews and Porter 1993; Scribner et al. 1997) were limited severely in inference by the use of protein electrophoresis. Alternatively, the use of microsatellite DNA markers provides increased precision suitable for examining microgeographic (<1.0 km) genetic patterns (Anderson et al. 2002; DeYoung and Honeycutt 2005). Comer et al. (2005) conducted the only published microgeographic investigation of spatial genetic structuring in white-tailed deer employing microsatellite DNA markers. They observed a low degree of genetic structuring in the population that was attributed to a young female age structure due to heavy hunting pressure, and a possible elevated dispersal rate of young female white-tailed deer on their study site. Work utilizing microsatellite DNA markers to examine microgeographic genetic structure in white-tailed deer populations under more traditional management regimes that commonly occur throughout the range of white-tailed deer is lacking. Microgeographic social and genetic structure in female white-tailed deer has substantial implications for disease transmission, evolutionary processes, and behavior-based strategies to alleviate human-wildlife conflicts. Therefore, we believe that additional research utilizing microsatellite DNA markers is warranted.

Our overall study objective was to examine the microgeographic genetic and social structuring in a free-ranging, non-migratory, and high density white-tailed deer herd in the central Appalachian Mountains of West Virginia, characteristically representative of many populations in the eastern United States. We used data from 14 microsatellite DNA loci and spatial autocorrelation analysis to: 1) examine the relationship between spatial distance and genetic relatedness for adult females on the study site, 2) determine relatedness among adult females within social groups delineated by visual observations, and 3) examine the relationship between spatial distance and genetic relatedness among social groups and their members.

Materials and Methods

Study site.—Our research was conducted on the 3,413 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) located in Randolph County, West Virginia (38°42’N, 80°3’W). The MWWERF was established in 1994 to investigate the relationship between industrial forestry and ecosystem processes. The MWWERF is located in the Unglaciated Allegheny Mountain and Plateau Physiographic province, and topography consists of plateau-like ridgetops with steep sides and narrow valleys (Smith 1995). Elevations range from 700–1,200m. The climate is moist and cool with mean annual precipitation in excess of 155 cm (Strausbaugh and Core 1977). The most common forest overstory cover is Allegheny hardwood-northern hardwood type composed mainly of American Beech (*Fagus grandifolia*), birch (*Betula* spp.), black cherry (*Prunus serotina*), maple (*Acer* spp.), and yellow-poplar (*Liriodendron tulipifera*). The proportion of the study site composed of forest regeneration areas ≤ 10 years of age increased from 8% to 14% during the study. Deer densities and sex ratios on the MWWERF during the study were estimated as 12-20 deer/km^2 and 6-18 adult males: 100 adult females, respectively (Langdon 2001). Males experienced high annual mortality from hunting, whereas females averaged approximately 85–90% annual survival (Campbell et al. 2005). Telemetry data revealed low levels (<5.0%) of dispersal in juvenile females (Campbell et al. 2004a). Abomasal parasite counts indicated the deer herd is approaching or has reached nutritional carrying capacity (Fischer 1996).

Deer capture.—To collect biological and movement ecology data, we captured deer from 27 February 1999–19 March 2005 using Clover traps (Clover 1954) baited with whole kernel corn. Captured animals were physically restrained, blindfolded, and given an intramuscular injection of xylazine hydrochloride (100 mg/ml, Cervizine®; Wildlife Laboratories Inc., Fort Collins, Colorado) at a dosage of 2.2 mg/kg body weight. We collected genetic samples, affixed large numbered plastic ear-tags (National Band and Tag, Newport, Kentucky), and estimated the age of immobilized animals via tooth wear and replacement (Severinghaus 1949). We outfitted captured animals with 3-year radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). Immobilization was reversed with a 12.0 mg intramuscular injection of yohimbine (5 mg/ml, Antagonil®; Wildlife Laboratories, Inc.). All animal handling procedures were approved by The University of Georgia Institutional Animal Care and Use Committee (Permit No. A2002-10119-0).

Collection of radiotelemetry and observation data.—From 7 April 1999 through 27 April 2005, we located radiocollared animals ≥ 2 times per week throughout the 24-hour day from permanent geo-referenced telemetry stations ($n = 591$), allowing ≥ 10 hours between telemetry locations. We used 4-element Yagi antennas and radio receivers (Advanced Telemetry Systems, Isanti, Minnesota) to estimate deer locations. We collected three to eight preliminary azimuths to pinpoint deer locations, and recorded two simultaneous azimuths that yielded an angle of 90 ± 40°. The LOCATE function of CALHOME was used to generate UTM coordinates of deer locations (Kie et al. 1996). To estimate telemetry error, we placed radiocollars at random geo-referenced sites in areas commonly used by deer (Samuel and Fuller 1996). Each researcher recorded an azimuth to a radiocollar from five telemetry stations. The resulting mean bearing error of -0.65° (SD = 8.41°) suggests that telemetry errors caused minimal bias in our telemetry protocol.

From 7 April 1999–27 April 2005, we recorded opportunistic visual observations of marked and unmarked animals along roadsides using 10x40 binoculars. Our observational data included date and time of observation, nearest geo-referenced telemetry station, sex, age class (juvenile or adult), size of group, and ear-tag numbers of marked animals. We considered individuals separated by ≤ 25 m to be associating (Aycrigg and Porter 1997).

Genetic analysis.—To investigate the genetic diversity of the overall population we collected whole blood or ear-notch tissue from captured deer and muscle tissue samples from fetuses obtained from deer euthanized for additional research purposes. Blood samples (2ml) were collected via jugular venipuncture and combined with 6ml of Longmire's solution (lysis buffer; Longmire et al. 1988) in Vacutainer® tubes (Benton Dickinson, Franklin Lakes, New Jersey) and stored at room temperature. Ear notch and muscle tissue samples were immediately placed in Vacutainer® tubes (Benton Dickinson) containing 8 ml of 95% ethanol, and allowed to fix at 4°C for ≥ 24 hours, after which they were stored at room temperature.

We extracted total DNA from samples using Qiagen® DNeasy™ Blood and Tissue Kit (Qiagen, Inc., Valencia, California). Standard protocols were used except that we allowed 24 hrs for tissue lysis by proteinase K, and only 100µl of buffer AE was added to the membrane of the mini spin columns. We stored extracted DNA samples in 1.5 ml microcentrifuge tubes (Fisher Scientific, Pittsburgh, Pennsylvania) at 4°C.

We selected a panel of 14 microsatellite loci from the 21 identified for use with white-tailed deer (Anderson et al. 2002, DeYoung et al. 2003b). The BM145, BM203, BovPRL, ETH152, K, OCAM, and R loci were omitted. We amplified DNA fragments by polymerase chain reaction (PCR) following methods by Anderson et al. (2002). The PCR products containing fluorescently labeled primers (6-FAM, HEX, or NED; Applied Biosystems, Foster City, California) and an internal size standard (GeneScan®-500 [ROX]™, Applied Biosystems) were subjected to capillary electrophoresis on an ABI PRISM® 3130 Genetic Analyzer (Applied Biosystems). Alleles were characterized by GeneMapper™ software (Applied Biosystems) followed by visual inspection and verification.

We used the identity analysis function of CERVUS 2.0 (Marshall et al. 1998) to detect inadvertent resampling of deer due to the loss of ear-tags. We additionally used the parentage analysis function of CERVUS 2.0 to estimate the mean genotyping error rate across all loci by comparing fetal samples to their known dams. Finally, we used CERVUS 2.0 to evaluate the loci for Hardy-Weinberg equilibrium (HWE), calculate allelic frequencies, expected heterozygosity, observed heterozygosity, and polymorphism information content (PIC).

Spatial autocorrelation analysis.— We conducted a spatial autocorrelation analysis via the program SPAGeDI 1.2 (Hardy and Vekemans 2002) to investigate the relationship between spatial distance (Euclidian distance) and genetic relatedness in adult female white-tailed deer. Spatial autocorrelation analysis can be applied to samples collected from continuously distributed populations to summarize the genetic variation in space (Dinez-Filho and Telles 2002). We used the Moran's *I* relatedness coefficient as the response variable and geographic distances (meters) between spatial coordinates was the explanatory variable. The Moran's *I* relatedness statistic was selected because it does not assume adherence to Hardy-Weinberg equilibrium (often unlikely in highly related populations), and provides high accuracy with moderate precision (Hardy and Vekemans 2002). We performed a jackknife procedure over loci to estimate standard errors for distance classes, and analyses were performed using 1,000 randomizations of spatial locations. We used one-sided tests for each distance class to determine if observed relatedness values were significantly greater than relatedness values from randomly permuted values. We performed three different types of spatial autocorrelation analyses to examine the social and genetic structuring of the population.

We first performed an autocorrelation analysis at the individual level for independently associated female deer. Only individuals ≥18 months of age were included in this analysis to reduce the risk of inflated spatial and genetic correlation from inclusion of juveniles (Coltman et al. 2003; Comer et al. 2005). We then assessed fine-scale structure for 21 distance classes ranging from 0–4,000 m at 200 m intervals, resulting in a minimum of 84 pair-wise comparisons per distance class (mean=1,142.0 m). We calculated distances between home range centers of individuals determined by the harmonic means of telemetry locations (Animal Movement extension v. 2.04; Hooge and Eichenlaub 1997) in Arcview GIS 3.3 (Environmental Systems Research Institute 1999). The coordinates from trap site locations obtained via a sub-meter global positioning system (GeoExplorer 3, Trimble Navigation Limited, Sunnyvale, California) were used for individuals lacking telemetry data.

Delineation of social groups.— We performed the final two autocorrelation analyses on female deer assigned to putative social groups. We considered marked animals members of a social group if they were visually observed associating together on a minimum of 60% of occasions, and were observed ≥ 2 times. Juveniles were not considered members of a social group until ≥18 months of age. We assigned members of a social group matching spatial coordinates representing the center of a social group's range based on visual observations.

We first conducted an autocorrelation analysis examining spatial distance and genetic relatedness between social groups at the individual level for eight distance classes ranging from

500-4,000 m at 500 m intervals. A minimum of 194 pair-wise comparisons were available per distance class (mean=559.1). Deer within social groups had the same spatial coordinates, hence they were not considered independent. We therefore performed no pair-wise comparisons between members of the same social group.

Additionally we conducted a spatial autocorrelation analysis at the population level to investigate the relatedness between entire social groups across six distance classes ranging from 750–4,500m at 750 m intervals. A minimum of 29 pair-wise comparisons were available per distance class (mean=62.5). We compared observed F_{it}, F_{st}, and F_{is} estimates with permuted values to examine allelic frequencies within social groups. We also calculated the R_{ho} relationship coefficient to measure the mean relatedness of individuals within social groups.

Results

A total of 420 unique multilocus genotypes was derived from white-tailed deer on the MWWERF. Most of these genotypes (346) were obtained from our trapped deer (80 male and 266 female); 74 were obtained from fetal tissue samples. Results from the identity analysis found two individuals with matching genotypes across all loci examined (n=13), and subsequent investigation of location and biological information confirmed the incidental resampling of one individual. Our mean observed genotyping error rate across loci was 0.0269 based on 74 fetal genotypes from 68 known parents. Of the 29 single locus offspring-parent mismatches, seven were identified as null alleles.

The 14 microsatellite loci examined in the population were highly polymorphic (Table 3.1). The number of alleles per locus ranged from 4 to 23, with a mean of 13.9. Mean expected heterozygosity for all loci was 0.786, and the mean polymorphism information content was 0.763. One locus (BM848) deviated from Hardy-Weinberg equilibrium (X^2, = 41.56, df =6,

$p<0.001$), perhaps due to the inclusion of highly related fetal samples in the overall population analysis (Anderson et al. 2002).

A total of 229 adult (≥18 months of age) female deer were used in spatial autocorrelation analysis at the individual level. The spatial coordinates used in the analysis were derived from telemetry locations for 139 of the individuals, and from capture sites for the 90 other individuals (Fig. 3.1). Mean (±SE) number of telemetry locations per individual was 219.9±13.3. We used 26,106 pair-wise distance comparisons in the analysis. The mean distance length between individuals was 2,467.7±13.3 m.

Spatial autocorrelation analysis of adult female deer indicated significant spatial genetic structuring. Moran's *I* relatedness coefficients declined as distance between pair-wise spatial locations increased (Fig. 3.2). The highest relatedness coefficient (0.088) was observed for individuals with the same spatial coordinates (e.g., same trap site), however a significant positive relatedness coefficient was detected for all distance classes ≤901.4 m. No significant difference was found between the observed relatedness coefficient and the randomly permuted value for the next distance class having a mean of 1,101.0 m. A negative relatedness coefficient was found in six of seven distance classes having mean geographical distances between 2,499.7–3,695.0 m.

We recorded total of 17,731 visual observations during our study. Of those, 2,831 observations were of identifiable animals. From these data, we delineated 28 putative social groups containing a total of 102 marked adult (≥18 months of age) females. Social groups contained a mean of 3.6±0.5 members, with a range of 2-12.

Our results from spatial autocorrelation analysis of social groups conducted at the individual level indicate significant genetic relatedness of individuals within social groups delineated by visual observations. The Moran's *I* relatedness coefficient between individuals within social groups was 0.090, which is a value similar to that of first cousins. When individual deer were not compared to other members of their social group, genetic similarity declined rapidly and became non-significant at a distance somewhere between 0 and 373.6 m (Fig. 3.3). A significant positive relatedness coefficient was also detected for two distance classes with means of 1,783.7 and 3,786.4 m, however the observed Moran's *I* relatedness coefficients were low (≤ 0.018) indicative of Type I errors. A significant negative relatedness coefficient was found in the distance classes having a mean distance of 2,776.8 m.

Our analysis of social groups conducted at the population level detected significant differences ($P<0.05$) in observed F_{it}, F_{st}, and F_{is} values compared to randomly permuted values. The positive observed F_{it} value (0.0297) indicates a deficit of heterozygosity at the population level, due to combining social groups into a single sample. The positive observed F_{st} value (0.0757) indicates significant genetic structure among populations (i.e. social groups). However, a negative F_{is} value (-0.0497) indicates greater heterozygosity within groups than would be expected by Hardy-Weinberg equilibrium. The observed R_{ho} relationship coefficient (0.1470) between individuals within social groups differed ($P<0.01$) from mean permuted values indicating relatedness among members of the same social group.

Discussion

The results from our spatial autocorrelation analysis conducted at the individual level illustrate the strong relationship between spatial location and genetic relatedness among adult female white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest. The pair-wise comparisons demonstrated that individuals with similar spatial coordinates were much more likely to be related than individuals with dissimilar spatial coordinates (i.e., greater geographic distance). Moreover, our results indicate spatial clustering of related individuals consistent with matriarchal social groups.

The graphical representation of our spatial autocorrelation results for individuals (Fig. 3.2) is strikingly similar to the hypothetical correlogram depicting a stabilizing profile proposed by Dinez-Filho and Telles (2002). This type of correlogram occurs when only short distance autocorrelation is found, and indicates that spatial genetic variation occurs in patches (Dinez-Filho et al. 2003). Because our spatial autocorrelation analysis was significant at the mean spatial distance of 901.4 m but not in the next distance class of 1,101.0 m, we can conclude that our patches are approximately 1,000 m in size.

Our findings differ from those of Comer et al. (2005). They reported a low degree of spatial genetic structuring at the individual level among female deer on the Savannah River Site in South Carolina. The lack of spatial genetic structuring was attributed to a young female age structure in the population due to heavy hunting pressure, and a possible elevated dispersal rate of young female white-tailed deer on their study site.

Aycrigg and Porter (1997) hypothesized that sociospatial behavior of white-tailed deer largely was dependent on the ability of a population to develop a complex age structure. Female deer on our study site have high annual survival (85–90%; Campbell et al. 2005), which may result in our low observed rates of female dispersal (<5.0%; Campbell et al. 2004). If herd management on our study site was altered towards population exploitation, future results may be similar to those reported by Comer et al. (2005). Similarly if juvenile female dispersal rates were as elevated as reported by Nixon et al. (1991), patterns of spatial genetic structure perhaps would not be present.

Our analysis of social groups delineated by visual observations provided further evidence of female social structuring on our study site. The Moran's *I* relatedness coefficient between social group members was 0.090, which is a value similar to that of first cousins. However, when individual deer were not compared to other members of their social group, genetic similarity declined rapidly and became non-significant at a distance somewhere between 0 and 373.6 m (Fig. 3.3). The observed F_{st} and R_{ho} statistics also indicated that members of social groups were significantly related.

Nonetheless, the negative F_{is} value indicates a higher level of heterozygosity within social groups than would be expected by Hardy-Weinberg equilibrium. This reflects the fact that group members are not sired by the same male, which is consistent with current understanding of white-tailed deer biology. Mathews and Porter (1993) also observed an excess of heterozygosity within delineated social groups on a New York study site. Still, we conclude that per-generational gene flow remains sufficiently restricted to generate positive local genetic structure despite polygynous breeding by males.

The ultimate mechanism responsible for our findings is spatial fidelity of matrilineal social groups resulting from high philopatry of female offspring. In a seasonally migratory deer herd, Mathews and Porter (1993) hypothesized that if female philopatry is responsible for spatial genetic structuring in white-tailed deer, then there would be an association between the genetic relatedness and spatial distance among social groups. However, they found no evidence for this association on breeding ranges; only on separate winter ranges. They reported that the overlap of social groups on breeding ranges masked the expected negative relationship between genetic relatedness and spatial distance.

Because the white-tailed deer population on our study site is non-migratory, we based our assignment of individuals into putative social groups exclusively on an extensive dataset of visual observations. We caution that interpretation of spatial genetic structuring analyses of non-migratory white-tailed deer should be accompanied by observational data because of the potential for spatial overlap of social groups, even in populations with high female philopatry.

Mathews (1989) described female social group formation as a series of juvenile female home ranges overlapping an older female's home range. This theory of population expansion requires highly philopatric female offspring, and assumes that social groups expand outward with each new female added. A previous investigation of home range size on our study site found that the summer home range of an adult female was 81.5 ha (Campbell et al. 2004b). Assuming a circular home range, the radius of an adult female is 509 m, or approximately half the distance at which genetic relatedness becomes non-significant (≈1,000 m). Therefore, the description of a central matriarch whom's home range is overlapped by the home ranges of female offspring as proposed by Mathews (1989) clearly is substantiated on our study site by genetic and radio-telemetry data.

Due to the social organization of deer, Porter et al. (1991) proposed that removing one or more of these social groups (i.e. localized management) would create an area of reduced deer density for >10 years. The results from our investigation of microgeographic spatial and genetic structure in a free-ranging, non-migratory, and high density white-tailed deer population support the underlying basis for localized management. Nevertheless, we suggest additional investigation of the applicability of localized management due to the behavioral plasticity of deer in response to varying demographic parameters (Comer et al. 2005; Miller 1997).

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TABLE 3.1.—Locus name, number of individuals typed (n), number of alleles, observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphism information content (PIC) for 14 microsatellite DNA loci amplified for 420 white-tailed deer from the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia from 1999–2005.

Locus	n	Alleles	H_o	H_e	PIC
BL25	417	4	0.405	0.416	0.386
BM4208	359	20	0.905	0.918	0.911
BM6438	405	16	0.822	0.886	0.875
BM6506	414	15	0.870	0.878	0.866
BM848[a]	375	15	0.800	0.880	0.867
Cervid1	409	17	0.851	0.868	0.853
D	408	11	0.772	0.812	0.787
ILSTS011	347	7	0.576	0.592	0.546
INRA011	412	8	0.556	0.560	0.516
N	405	22	0.854	0.911	0.904
O	409	9	0.685	0.655	0.587
OarFCB193	318	14	0.912	0.879	0.868
P	403	14	0.846	0.847	0.829
Q	415	23	0.841	0.900	0.890

[a] Locus not in H-W equilibrium ($P<0.001$)

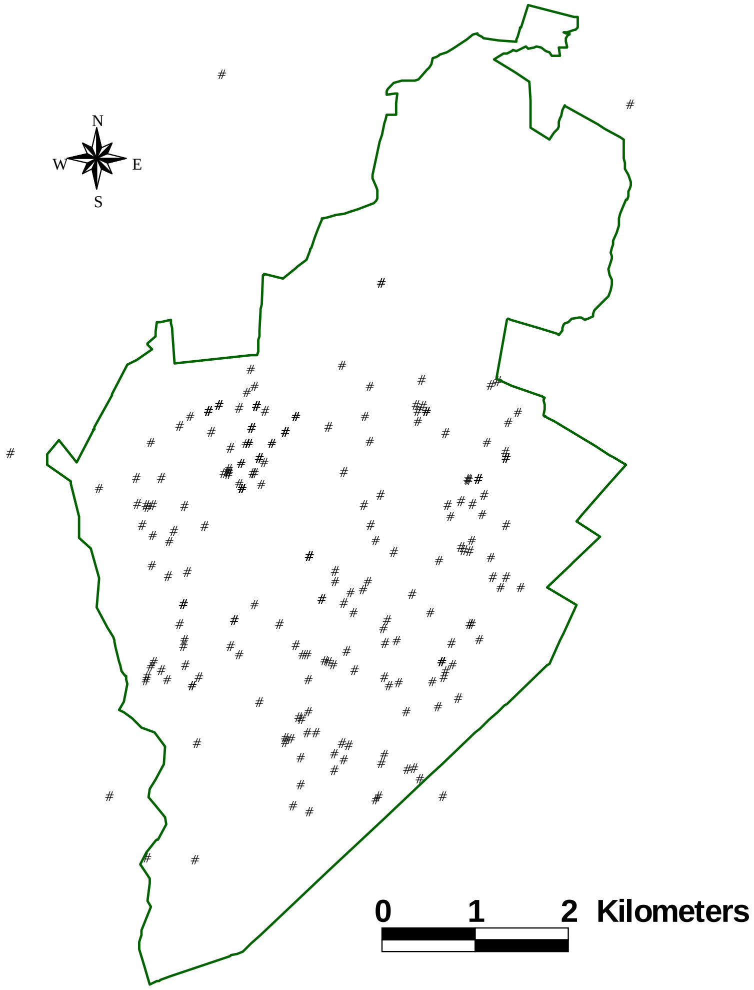

FIG. 3.1.—Spatial locations (black dots) of 229 adult (≥18 months of age) female white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia from 1999–2005 used in spatial autocorrelation analysis. The solid line represents the boundary of the study area.

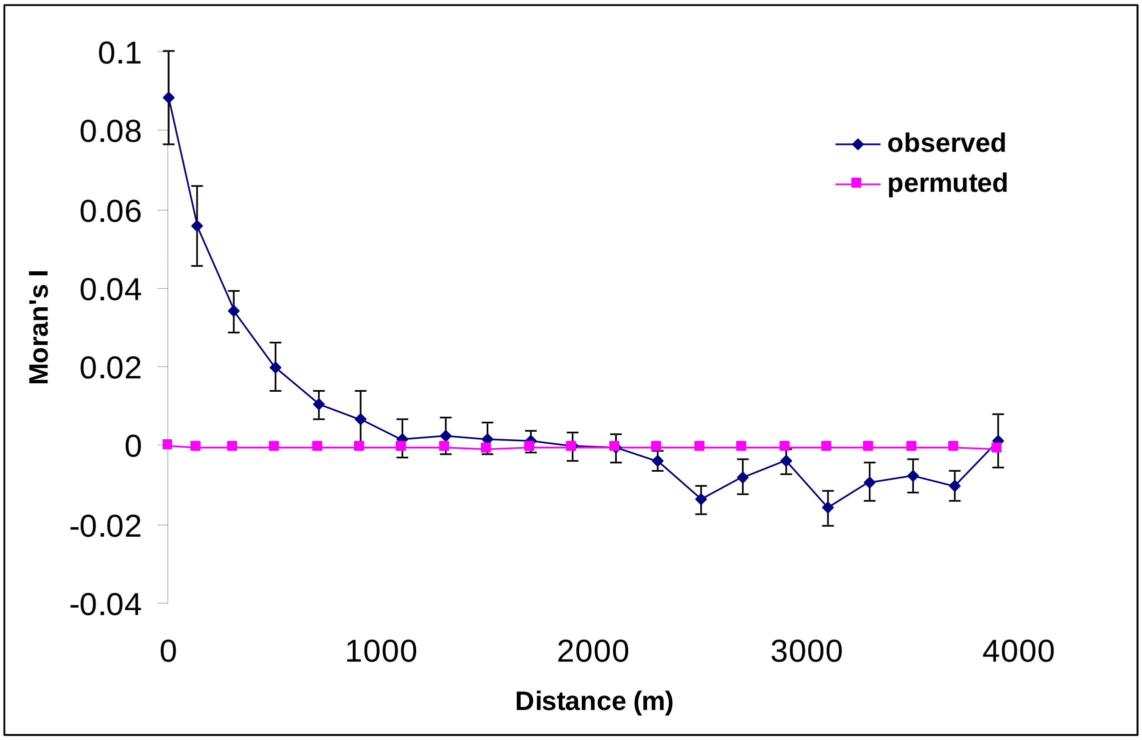

FIG. 3.2.—Mean (±SE) pair-wise relationship coefficients (Moran’s *I*) by distance for 229 adult (≥18 months of age) female white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia from 1999–2005.

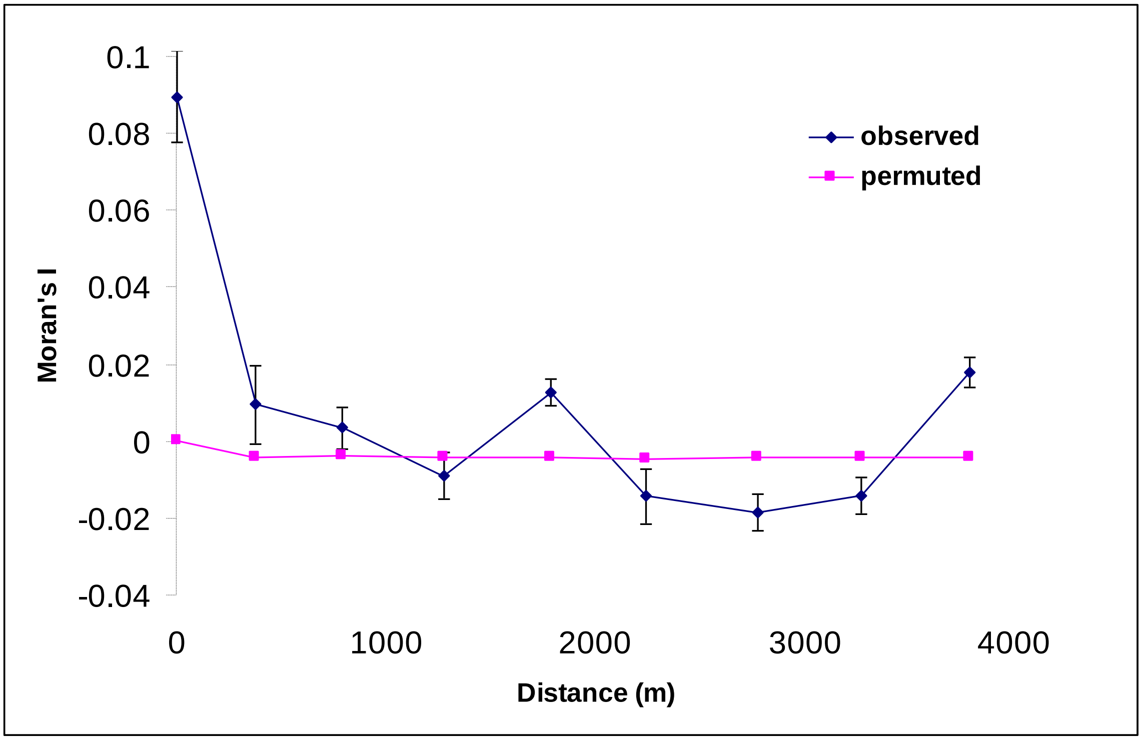

FIG. 3.3.— Mean (±SE) pair-wise relationship coefficients (Moran's *I*) by distance between members of 28 social groups delineated by visual observations on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia from 1999–2005. A total of 102 adult (≥18 month of age) female white-tailed deer was used in the analysis.

CHAPTER 4

A TEST OF LOCALIZED MANAGEMENT FOR REDUCING WHITE-TAILED DEER HERBIVORY IN CENTRAL APPALACHIAN REGENERATION SITES[1]

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[1] Miller, B. F., T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. To be submitted to the *Journal of Wildlife Management*.

Abstract: White-tailed deer (*Odocoileus virginianus*) herbivory in forest regeneration sites can have profound impacts on current and future stand structure, species composition, and biodiversity. Removal of deer social units (localized management) has been proposed as a strategy to alleviate deer overbrowsing in forest systems. We conducted an experimental localized removal in a high-density deer population in the central Appalachians of West Virginia during Winter 2002. We removed 51 deer within a 1.1 km^2 area that encompassed 2 forest regeneration sites (14 ha). During the summer following removal, significant decreases in distance from the removal area were detected in 8 of 30 (26.7%) adult females having pre-treatment mean telemetry locations <2.5 km from the center of the removal area. Browse data were collected during the summers of 2001–2004 from forest regeneration sites to examine the impacts of localized management. Herbivory rates declined annually in both the removal and control areas, due in part to increased timber harvesting on the larger study site, suggesting that increasing forage availability may be more effective at reducing impacts on forest regeneration than localized reductions in deer populations. Three years after the initial removal, we removed an additional 31 deer from the original 1.1 km^2 removal area. The home range shifts of adjacent deer coupled with the large number of animals collected in the second removal suggests that localized management only produces temporary voids within high-density deer herds.

Key words**:** Appalachians, forest regeneration, herbivory, localized management, *Odocoileus virginianus*, rose-petal hypothesis, West Virginia, white-tailed deer.

INTRODUCTION

The successful recovery of white-tailed deer (*Odocoileus virginianus*) populations in the eastern United States has resulted in a variety of social and ecological conflicts. Overabundant deer populations can result in deer-vehicle collisions, depredation of agricultural crops, and damage to ornamental plantings (Conover 1997). Excessive herbivory also can have negative effects on forested ecosystems (McShea and Rappole 1997a), particularly in regenerating forests because long-term successional patterns may be altered (Marquis 1981, Horsley and Marquis 1983, McWilliams et al. 1995). Shifts in species composition, reduced stocking, extended rotation lengths, and entire regeneration failures are possible on some sites (Marquis 1974, Tilghman 1989, Horsley et al. 2003).

Although regulated hunting can effectively control deer populations in many situations, managing deer populations at a regional or even county level may not control locally overabundant populations (Waller and Alverson 1997, McShea and Rappole 2000). Additionally, using hunting as a management tool may not be applicable in all situations. Hunter access is often restricted in suburban areas or public parks because of safety concerns or regulatory constraints (Warren 1991, McShea and Rappole 1997b).

Alternative techniques for controlling deer populations and reducing their negative effects have been tested but often are cost-prohibitive, (e.g., translocation; Beringer et al. 2002), require substantial effort and interval of time before population densities are reduced (e.g., fertility control; Merrill et al. 2006), or may be viewed unfavorably by the public (e.g., sharpshooting; Stout et al. 1997). As a result natural resource managers must explore novel approaches for reducing the impacts of overabundant deer populations.

Recent research investigating the sociobiological characteristics of female deer has warranted its consideration in management efforts. Mathews (1989) indicated that female social groups are structured as a series of overlapping home ranges centered on a matriarchial female. The theoretical shape of these social units is similar to the petals of a rose, and has been termed the "rose-petal hypothesis". This model of social structuring and population expansion has led researchers to question traditional concepts for deer management that often emphasize population reductions on a large geographical area.

Accordingly localized management has been proposed as a management tool that exploits the social structuring of deer (Porter et al. 1991, Mathews and Porter 1993, McNulty et al. 1997). This technique involves the "surgical" removal of a matriarchal social group(s) from a limited geographical area to create a 10–15 year period of reduced deer densities (Porter et al. 1991). The effectiveness of the technique depends on the suitability of the rose-petal hypothesis as a model for population expansion. Specifically, deer populations must have low female dispersal, be highly philopatric, and display high site fidelity for localized management to be applicable.

McNulty et al. (1997) conducted an experimental test of the localized management technique on a low density (2–6 deer km^2), migratory, and unhunted deer population in the Adirondack Mountains of New York. In that study, 14 deer were removed from a 1.4 km^2 area, and no adjacent female deer (n=9) recolonized the area within 2 years of monitoring. A subsequent examination of the same removal area by Oyer and Porter (2004) approximately 6 years post-removal reported reduced deer densities for a period of 5 years. These results suggest that localized management may be a viable technique to prevent overbrowsing by deer in areas where traditional approaches are unsuitable. Possible sites for applying localized management include urban/suburban areas (Porter et al. 2004, Kilpatrick et al. 2001) or parks (Porter et al.

1991). Forest regeneration sites located in remote areas where access to the hunting public is difficult or problematic also may benefit from an application of localized management prior to timber harvesting to ensure successful regeneration (Campbell et al. 2004). However, the effectiveness of any behavior-based management technique may be limited by the behavioral plasticity of white-tailed deer (Comer et al. 2005, Miller 1997).

Campbell et al. (2004) assessed the feasibility of implementing localized management on a hunted, non-migratory, and high-density deer herd in the central Appalachian Mountains of West Virginia. They reported that the *a priori* assumptions of localized management were met, and that a test of localized management on the study site would be possible. Herein we report on the results of that test of localized management and its effectiveness in reducing herbivory rates of forest regeneration areas.

STUDY AREA

Our research was conducted on the 3,413 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) located in Randolph County, West Virginia (38°42'N, 80°3'W). The MWWERF was established in 1994 to investigate the relationship between industrial forestry and ecosystem processes. The MWWERF is located in the Unglaciated Allegheny Mountain and Plateau Physiographic province, and topography consists of plateau-like ridgetops with steep sides and narrow valleys (Smith 1995). Elevations range from 700–1,200m. The climate is moist and cool with mean annual precipitation in excess of 155 cm, most of which falls as snow in the winter months (Strausbaugh and Core 1977). Soils of the MWWERF are acidic, well-drained Inceptisols (Schuler et al. 2002).

Forest types on the MWWERF are naturally regenerated second-growth stands established in the early 1900's following extensive area-wide railroad logging (Clarkston 1993).

Currently the forests are managed primarily by even-aged harvesting with an 80-100 year rotation length (Adams 2005). Regeneration sites of approximately 15 ha are well distributed throughout the MWWERF.

The most common overstory cover is Allegheny hardwood-northern hardwood forest type composed of American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and black cherry (*Prunus serotina*). Cove hardwoods and mixed-mesophytic forests composed of yellow-poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*), sweet birch (*Betula lenta*), and northern red oak (*Quercus rubra*) are common at lower elevations. Eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*) comprise a significant portion of the forest cover on elevations over 1,000 m and along sheltered riparian zones. A shrub layer and understory groundcover is absent in many areas with the exception of rhododendron (*Rhododendron maximum*) thickets in upland an riparian areas, and thick mats of hay-scented fern (*Dennstaedtia punctilobula*) in areas where the canopy is interrupted and sunlight reaches the forest floor.

Intensive research of the deer population on the MWWERF began in 1999 (Campbell 2003). Deer densities and sex ratios on the MWWERF at the time of the study were estimated as 12-20 deer/km^2 and 6-18 adult males: 100 adult females, respectively (Langdon 2001). Male deer experience high annual mortality from hunting, whereas females average 85–90% annual survival (Campbell et al. 2005). Telemetry data indicates low (<5.0%) dispersal of juvenile females (Campbell et al. 2004). Abomasal parasite counts indicate the deer herd is approaching or has reached nutritional carrying capacity (Fischer 1996).

METHODS

Deer Capture and Radiotelemetry

To collect preliminary biological and movement data, we captured 224 deer (51 males and 173 females) from January through April during 1999-2001 using Clover traps (Clover 1954) and rocket nets (Hawkins et al. 1968) baited with whole kernel corn. Captured animals were physically restrained, blindfolded, and given an intramuscular injection of xylazine hydrochloride (100 mg/ml, Cervizine®, Wildlife Laboratories, Inc.) at a dosage of 2.2 mg/kg body weight. We affixed large numbered plastic ear-tags (National Band and Tag, Newport, Kentucky), collected genetic samples, and estimated the age of animals via tooth wear and replacement (Severinghaus 1949). We outfitted 3-year radiocollars (Advanced Telemetry Systems, Isanti, Minnesota) to 192 captured animals. We reversed immobilization with a 12.0 mg intramuscular injection of yohimbine (5 mg/ml, Antagonil®, Wildlife Laboratories, Inc.). All animal handling procedures were approved by The University of Georgia Institutional Animal Care and Use Committee (Permit No. A2002-10119-0).

We located radiocollared animals ≥ 2 times per week throughout the 24-hour day from permanent geo-referenced telemetry stations, allowing ≥ 10 hours between telemetry locations. We used 4-element Yagi antennas and radio receivers (Advanced Telemetry Systems, Isanti, Minn.) to estimate deer locations. We collected 3–8 preliminary azimuths to pinpoint deer locations, and recorded 2 simultaneous azimuths that yielded an angle of 90 ± 40°. We used the LOCATE function of CALHOME to generate UTM coordinates of estimated deer locations (Kie et al. 1996). To estimate telemetry error, we placed radiocollars at random geo-referenced sites in areas commonly used by deer (Samuel and Fuller 1996). Each researcher recorded an azimuth to a radiocollar from 5 telemetry stations. The resulting mean bearing error of -0.65° (SD = 8.41°) suggests that telemetry errors caused minimal bias in our telemetry protocol.

Removal Area Determination

We selected the removal area based upon its feasibility and suitability for an application of localized management. Laseter (2004) conducted an analysis of telemetry, genetic, and observation data of deer on our study site prior to the initiation of the removal. Based on home ranges and activity centers derived from 20,587 telemetry locations for 127 females and genetic data from 56 of those females, it was determined that the spatial scale of microgeographic variation was approximately 500 meters. Additionally, putative social groups were identified on the study site, and verified with genetic and observation data.

We selected one of the social groups identified by Laseter (2004) for removal. We placed the center of the intended removal area in a location central to the social group based on telemetry data. A 1.1 km^2 circular removal area having a 600 m radius was selected to encompass the targeted animals, and approximate the spatial scale of genetic variation previously determined. Additionally, 2 regeneration sites were within the proposed removal area to evaluate the effects of localized management on herbivory.

Initial Removal

From 7 January to 27 February 2002, we captured deer in modified Clover traps baited with whole kernel corn (Clover 1954). We distributed 14 traps throughout the removal area (Fig. 4.1). Traps were checked twice daily, and trapped deer were physically restrained and given an intramuscular injection of 20.0 mg of succinylcholine chloride (20mg/ml, Anectine®, Burroughs Wellcome Co., Research Triangle Park, NC). After recumbency, animals were immediately euthanized by bolt-gun (Cash Special, Accles and Shelvoke Ltd., Birmingham, England).

Periodic sharpshooting also was conducted by West Virginia Department of Natural Resources personnel to remove trap-reluctant individuals after 4 weeks of trapping.

We removed lower mandibles from all animals and ages were estimated by tooth wear and replacement (Severinghaus 1949). All carcasses were taken to the West Virginia Division of Natural Resources Captive Animal Facility and Wildlife Park in French Creek, WV and fed to captive carnivores. We recorded person-hours expended during removal and carcass processing activities.

We determined when to cease removal efforts by examining trapping data and conducting deer track count surveys in the snow. We established a transect that originated 1,800 m northeast of the center of the removal area, crossed through the removal area, and terminated 1,800 m southwest from the center of the removal area to detect changes in deer density. We recorded elapsed time since the last snowfall, or elapsed time since the last track count. All tracks were swept away after each survey. We conducted 6 track counts before initiating the removal, 11 track counts during the removal period, and 4 track counts after the removal period. The locations of all tracks that crossed the transect were recorded with a sub-meter global positioning system (GeoExplorer 3, Trimble Navigation Limited, Sunnyvale California), obtaining a minimum of 30 positions per point. We determined the distance from each track to the center of the removal area using ArcView 3.3 (ESRI 2002).

Monitoring of Radiocollared Deer

We examined the summer telemetry data (May to September) of 30 female deer (1–8+ years old in 2001) monitored during both pre- and post-removal years (2001 and 2002, respectively) to identify treatment-related movements. Only those deer having pre-removal mean distances to the center of the removal area of <2.5 km were included in our analysis. We determined the distance from each telemetry location to the center of the removal area using the Animal Movement extension v. 2.04 (Hooge and Eichenlaub, 1997) in Arcview GIS 3.3 (ESRI 2002) for deer monitored throughout the summer and having ≥25 locations.

We performed 2 statistical tests to evaluate treatment-related movements. We first performed Fisher's distribution-free sign test (Hollander and Wolfe 1973:39–40) to test for differences in mean pre- and post-removal distances from telemetry locations to the center of the removal area. The sign test compares the number of animals with smaller post-removal distances (i.e., moved closer to removal area) with the number of animals with larger post-removal distances (i.e., moved away from removal area). If there is no treatment effect, then the number of animals in each category should be similar. We then performed a 2-tailed unequal variance 2-sample *t*-tests (Ruxton 2006) on ranked distances for each individual to determine if the mean location distances in the year after treatment application differed from the distances prior to treatment application.

To investigate movements without any treatment effects, we compared the distances from telemetry locations to the proposed center of the removal area from the two summers prior to application of localized management (2000 and 2001) as previously described for 27 female deer (1–8+ years old) with mean distances from telemetry locations to the center of the removal area of <2.5 km. All statistical procedures were performed using SAS (SAS Institute 2004), and results were considered significant if $P < 0.05$.

Vegetation Sampling

To examine the effects of the localized removal on herbivory rates, we assessed pre-treatment deer browsing data in 2001 from 6 regeneration sites each approximately 14 ha in size. Two regeneration sites were located within the removal area, 2 regeneration sites were located

1.1 and 1.3 km, from the center of the removal area to serve as near controls, and 2 other regeneration sites located 2.6 and 2.7 km from the center of the removal were designated as far controls (Fig. 4.2). All regeneration sites were resampled in 2002, 2003, and 2004 except the far control regeneration sites that were not resampled in 2004. The two regeneration sites within the removal area were in their first and third growing seasons during the first year of vegetation sampling. The two near control regeneration sites were of identical ages, however the two far control regeneration sites were both in their second growing seasons during the first year of vegetation sampling.

We systematically distributed 30 $1 m^2$ permanently marked sampling plots along the edge of skidder trails throughout each regeneration area. Mean distance between each plot was 121 m. We matched an "interior plot" to each trail plot 5 m from the skidder trail in the most perpendicular cardinal direction. All plots were sampled between 15 July and 15 August of each study year. Within each year we sampled plots within ± 7 days of the original sampling date in 2001 to prevent temporal bias due to changes in vegetation structure, species composition, or herbivory rates.

Within each plot, we recorded the total number of browsable units of each species ≤ 1.5 m from the ground (i.e., available), and the total number browsed following Ford et al. (1993). We determined a browsing rate for each sampling plot by dividing the number of twig tips browsed by the total number available. All browsing was assumed to be caused by white-tailed deer because no herbivory by other vertebrates was detected.

We determined the effect of deer removal on changes in browsing rates while accounting for correlation among years by using a repeated measures multiple analysis of variance (MANOVA) in SAS using the GLM procedure (SAS Institute 2004). We used a profile analysis procedure to investigate the interaction of time period and treatment by examining parallelism, levels, and flatness of browsing rates between years (Von Ende 1993).

We used an analysis of variance (ANOVA) where treatment was the main effect to compare browsing rates among treatments within a time period. Tukey's honestly significant difference multiple range test (SAS Institute 2004) was performed if differences among treatments were detected. A 2-sample t-test was performed on data from the final time period to compare herbivory rates between the 2 treatments. Trail and interior plots were pooled for analysis. We transformed browsing percentage data using an arcsine square-root transformation (Dowdy et al. 2004).

Second Removal

We conducted a second removal between1 January to 21 February 2005, 3 years after the initial removal. We implemented the second removal to compare the number of animals captured, and effort required with the initial removal. Additionally we collected genetic samples for future comparison with the individuals captured in the initial removal. We utilized the same trapping methods and duration as the initial removal. We also recorded person-hours expended collecting biological information from carcasses and cleaning of processing facilities.

RESULTS

Initial Removal

We removed 51 deer ranging in age from 0.5-8.5+ years (Fig. 4.3) from the 1.1 km^2 targeted area during the 8 week period. The number of individuals removed per week was negatively related to the duration of trapping (Fig. 4.4). Females comprised the majority of the animals (39 of 51), with a mean (± SE) age of 3.7 ± 0.4 years. The mean age was lower for males (0.9±0.3 years old) because most males were fawns (9 of 12). Male ages ranged from 0.5–3.5 years old.

Results from our track counts conducted before, during, and after the removal indicated a negative relationship between deer density and the duration of trapping. The mean number of tracks recorded within the removal area was 22.2 ± 7.0 tracks/10 hours during the pre-removal period. The number decreased to 5.6 ± 1.2 tracks/10 hours during the removal and 2.5 ± 1.5 tracks/10 hours post-removal. Of the 9 radiocollared females with home ranges encompassing a portion of the removal area, 8 were removed. No radiocollared deer having home ranges outside of the removal area were captured.

A total of 467 person-hours were required for the initial removal. Preparing trap sites and pre-baiting required 24.7 person-hours. The majority of the effort was expended checking traps, removing trapped animals, and sharpshooting efforts. These activities required 442.5 person-hours, almost 95% of the total person-hours expended. A mean effort of 9.2 person-hours/deer removed was required.

Monitoring of Radiocollared Deer

Excluding the single radiocollared female that was not removed, we recorded 6,630 telemetry locations from 84 extant radiocollared deer (1 male and 83 female) each having ≥34 locations from 18 February 2002 to 20 December 2002 (Fig. 4.5). The mean distance from all telemetry locations to the center of the removal area was 2,607.3 ± 10.2 m (range = 96.4–5,433.8 m). There were 11 telemetry locations within the removal area from 10 different deer. The proportion of each animal’s telemetry points that occurred within the removal area averaged 1.4 ± 0.04% (range = 1.1–2.4%) of all telemetry points.

The mean number of telemetry locations for deer in the pre-removal and post-removal periods was 29.3 ± 0.3 (range = 26–32) and 38.5 ± 0.6 (range = 28–44), respectively. Of the 30 female deer having mean distances from telemetry locations to the center of the removal area of <2.5 km, 19 of them (63.3%) had smaller distances in the summer following the removal treatment. Results of the sign test comparing deer with smaller post-removal distances to those with larger post-removal distances approached statistical significance (z = 1.46, P = 0.072).

Differences between pre-removal and post-removal distances to the center of the removal area were detected by *t*-tests in 8 of 30 (26.7%) deer (Fig. 4.6). All significant differences in distances to the removal area were of deer moving closer to the removal area; no significant movements away from the removal area were detected. The mean difference in pre- and post-removal distances of the 8 animals was 136.3 ± 13.2 m (range = 57.7–171.1 m) closer to the center of the removal area.

The mean number of telemetry locations collected from deer in the 2 summers prior to the application of localized management (2000 and 2001) was 65.0 ± 0.4 (range = 59–69) and 29.4 ± 0.3 (range = 25–32), respectively. The sign test detected no significant differences between distances from telemetry locations to the center of the proposed removal area for the 2 summers (z = 0.96, P = 0.17). Differences in distances were detected by *t*-tests in 5 of 27 (18.5%) deer. Of those 5 animals, 4 moved closer to the removal area, and one moved further away. The mean difference in pre- and post-removal distances of deer moving closer and moving farther away was 132.6 ± 9.8 m (range = 103.8–148.0 m) and 99.5 m, respectively.

Herbivory Data

We recorded browsable units from a total of 38 woody, and 4 semi-woody plant species. However, 12 species constituted 85.0% of the available browsable units (187,560 of 220,631) recorded in our study. These included species representative of the woody overstory present prior to timber harvesting such as black cherry, red maple, sugar maple, birch, magnolia (*Magnolia fraseri* and *acuminata*), American beech, yellow-poplar, northern red oak (*Quercus rubra*), and witch-hazel (*Hamamelis virginiana*). Three early successional invaders such as fire cherry (*Prunus pensylvanica*), striped maple (*Acer pensylvanicum*), and blackberry (*Rubus* spp.) increased in abundance following timber harvesting.

Herbivory rates for all woody and semi-woody species combined decreased annually among the 3 treatments (Fig. 4.7). Herbivory rates in the removal area, near control, and far control decreased 71.7%, 50.0%, and 43.5% from the pre-removal summer to the first summer post removal (SPR), respectively. The rate of decrease did not differ among treatments ($F_{2,335}$ = 2.31, P = 0.10).

During the second summer post removal, the herbivory rate of the far control decreased an additional 51.4% from a mean herbivory rate of 7.4 ± 1.0% (n=118) to 3.6 ± 0.8% (n=120). During the same time period the herbivory rates of the near control and removal area decreased 9.9% and 9.3%, respectively. The rate of decrease differed among the 3 treatments ($F_{2,335}$ = 8.35, P < 0.001). However, the mean herbivory rate of the far control (3.6 ± 0.8%, n=120) did not differ from the herbivory rate of the removal area (3.9 ± 0.8%, n=119) in the second SPR ($F_{2,358}$ = 18.06, P < 0.001).

During the third summer post removal, herbivory rates further decreased 52.7% and 5.1% for the near control and removal area, respectively. The rate of decrease differed between the two treatments ($F_{1,236}$ = 14.60, P < 0.001). The mean herbivory rate did not differ between the near control (4.3 ± 0.9%, n=120) and the removal area (3.7 ± 1.0%, n=118) in the third summer post treatment (T_{236} = 1.35, P = 0.18).

Second Removal

Three years after the initial treatment, we removed an additional 31 deer from the original removal area (Fig. 4.8) using the same techniques as the initial removal. The number of deer removed per week declined as the duration of trapping increased (Fig. 4.4). Females comprised the majority of the animals removed (26 of 31). The mean age females was 4.5 ± 0.5 years (range = 0.5–8.5+). Eighteen of the females were ≥ 3.5 years of age.

All 5 males removed were fawns (0.5 years). One of the fawns had been captured by hand as a neonate in June 2004 and outfitted with an expandable radiocollar (Advanced Telemetry Systems, Isanti, Minnesota). His initial capture site and subsequent summer (n = 32) and fall (n = 18) telemetry locations occurred on the southwestern periphery of the removal area.

A total of 372.4 person-hours were expended during the second removal period. Preparing trap sites and pre-baiting required 6.9 man-hours. Checking traps, removing trapped animals, and sharpshooting efforts required a total of 365.5 person-hours. A mean effort of 12.0 person-hours/deer removed was required. Collecting biological data from carcasses and cleaning of processing facilities and equipment required an additional 2.4 person-hours per deer.

DISCUSSION

For localized management to be effective, a removal area must be sufficiently large to provide an opportunity for removal of an entire social unit. McNulty et al. (1997) reported that 14 of 17 animals from a known social group were successfully removed from a 1.4 km^2 area in the Adirondacks of New York. Their removal area size was calculated retrospectively based on home range analysis of the targeted deer. Prior knowledge of social structuring and movement data typically are not available, although this may not be necessary if deer exhibit high site fidelity and minimal female dispersal (McNulty et al. 1997). Therefore, management could hypothetically remove ≥ 1 social group if the area is large enough to encompass at least a portion of the home ranges of social group members.

Based on trapping success, track count data, and removal of radio-collared individuals, we estimate that >80% of the resident animals were removed within the 8-week removal period. Campbell et al. (2006) found that 89.5% (34 of 38) radio-collared deer utilized a bait site occurring within their home range during a 14–16 day observation period on the same area. We distributed Clover traps in our removal area at a density of 1 trap/ 8.1 ha. Although the visitation of bait sites may not be equivocal to deer use of Clover traps, we believe that placing multiple traps within the home range of each target animal greatly increased our removal success. Thus, our results demonstrate that a large proportion of deer in a high-density population can be removed from a 1.1 km^2 removal area by the combination of trapping and sharpshooting.

In the years following the application of localized management in the Adirondack Mountains, deer density declined to an area-wide estimate of 2 deer/km^2 because of severe winter weather (Oyer and Porter 2004). They reported that the reduced deer density persisted in the 1.4 km^2 treatment area persisted for approximately 5 years. Furthermore, Oyer and Porter (2004) concluded that all deer captured in their removal area were individuals missed during the removal efforts, or descendants of those deer.

The low initial deer density, and subsequent additional decrease in deer density of the Adirondack study are important differences between our study and that of Oyer an Porter (2004). The population density in the Adirondack study was estimated to be 6 deer/km^2 at the time of the removal (McNulty et al. 1997), whereas the density we observed was 12–20 deer/km^2 (Langdon 2001). Our removal of 51 deer from the 1.1 km^2 treatment area compared to the removal of 14 deer from a 1.4 km^2 treatment area in the Adirondack site is consistent with density estimates on our area being ≥3 times that of the New York study site.

The high densities we observed have substantial implications for the persistence of a population void. If initial deer densities in an area are low prior to an application of localized management, then only a small number of missed individuals will be left as population founders. However, in sites with high deer densities where human-deer conflicts often occur, and herd management is needed, even the most intense removal efforts may leave a sizable founding population.

Dispersal rates of juvenile females are critical to the effectiveness of the localized management technique (Porter et al. 2004). Localized management assumes that population density has little effect on female dispersal rates (Porter et al. 1991, McNulty et al. 1997). However, because of the high population density on our study area, there may be an increased chance of colonizing voids by female dispersal based on the high number of deer surrounding the removal area. Furthermore low female dispersal should not be assumed for all areas. High female dispersal rates have been reported in areas with heavy annual harvests and a young female age structure (Comer et al. 2005), as well as in fragmented agricultural landscapes (Nixon et al. 1991).

Site fidelity of adjacent adult females also is a critical component to the persistence of a population void. In the Adirondacks, no movements of adjacent animals were detected (Oyer and Porter 2004). We detected no immigration of adjacent animals in our study. However, no radiocollared animals with pre-treatment mean telemetry locations <1km from the center of the removal area survived removal efforts, with the exception of one missed adult female. Unboubtably our lack of immediately adjacent radiocollared deer is responsible for not detecting immigration of surviving individuals. Based on our telemetry data, 8 of 30 (26.7%) adult females having pre-treatment mean telemetry locations <2.5 km from the center of the removal area female deer were significantly closer to the removal area and none of the 30 animals had mean telemetry locations significantly further away from the removal area after the application of localized management. Therefore, we conclude that some shift of home-ranges occurred in response to the population void.

Our results suggest that encroachment from adjacent animals may reduce the persistence of removal effects in high density deer herds. Except for the single radiocollared adult female missed during the initial application of localized management, it is unknown how many deer were left as founding individuals. Of the 31 deer we removed 3 years later, 18 of them were alive at the time of the initial removal based on their estimated age. Their presence in the removal area is likely the result of some combination of dispersal into the area or shift from adjacent areas.

Based on the large number of deer removed three years after the initial removal, localized management provided, at best, only a short term reduction in deer densities. Although we removed 31 individuals within an 8-week trapping period, there were additional deer in the removal area after the conclusion of the second application of localized management. Approximately 3-weeks after the cessation of removal efforts, West Virginia Department of Natural Resources personnel observed at least 4 deer within the removal area, and collected an additional 2.5 year old female. Therefore a minimum of 35 animals resided in the removal area three years after the initial removal of 51 animals.

In the first summer after treatment application the greatest decline in herbivory rates was observed for the removal area, although the rate of decline was not statistically different from the other areas. This indicates that the deer removal may have reduced herbivory pressure in the removal area. However, the herbivory rates of the far control and near control areas also declined in the following summers until their herbivory rates did not differ from those within the removal area. Over the study period, the proportion of the study area composed of harvested areas <10 years old increased from 8% to 14%. Theoretically, increasing ecological carrying capacity by providing abundant forage across a landscape can reduce overall browsing pressure (Tilghman and Marquis 1989, Marquis et al. 1992, Ford et al. 1993, Kalen 2005). We believe this increase in natural forage was responsible for the declines in herbivory rates observed for all of the removal and control areas.

We conclude that although localized management may have provided a temporary reduction in herbivory rates, increasing forage availability may be a more effective means of minimizing the impact of deer herbivory on forest regeneration areas.

MANAGEMENT IMPLICATIONS

We found that the combination of trapping and periodic sharpshooting was effective for removing deer from a heavily forested remote area. However, our data suggest that a single application of localized management in high-density deer herds may only provide temporary reductions of deer-densities despite appearing to fulfill all *a priori* requirements for localized management. Repeated removals (every 2 years) or substantially increasing the sizes of removal areas may be necessary to counter the impacts of encroachment, dispersal, and reproduction of unharvested individuals in high-density deer populations.

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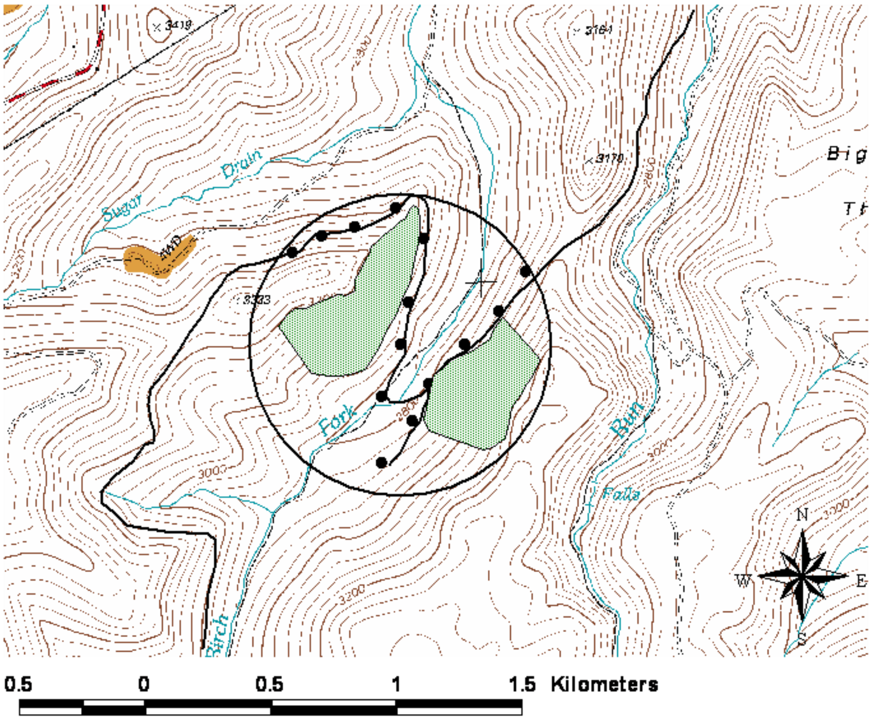

Fig. 4.1. The 1.1 km^2 deer removal area (circular area) implemented from 7 January to 27 February 2002 on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA. Black dots indicate the location of Clover traps. Shaded areas are forest regeneration sites.

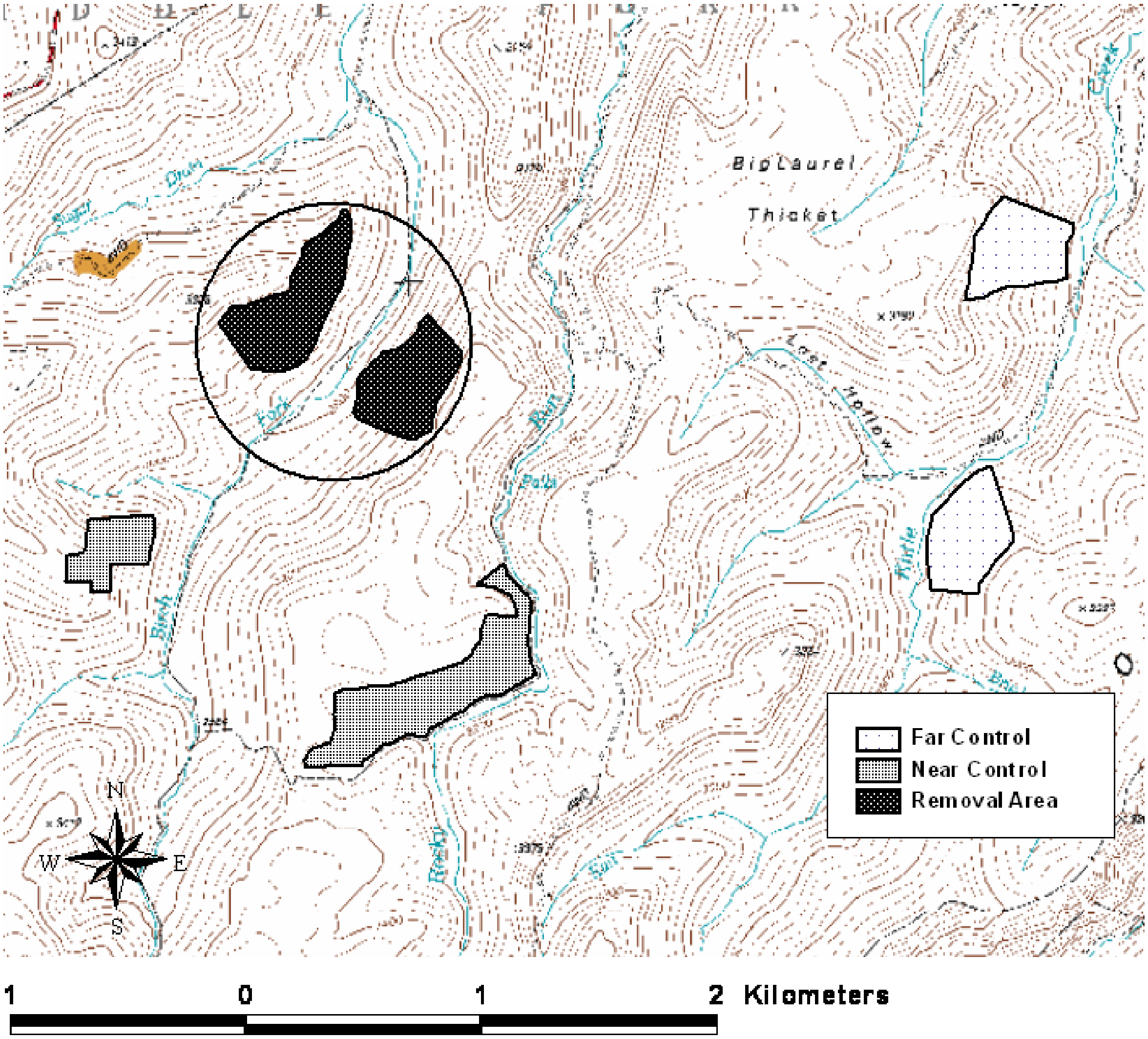

Fig. 4.2. Locations of 6 forest regeneration sites where herbivory was measured on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA from 2001–2004. Regeneration sites were assigned to 1 of 3 categories (Removal Area, Near Control, and Far Control) for analysis. The circular area represents the 1.1 km^2 removal area where the treatment was applied.

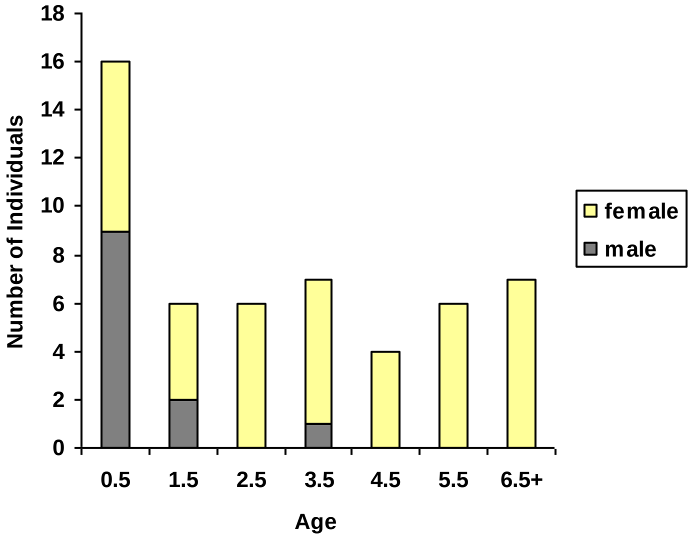

Fig. 4.3. Estimated ages of male and female white-tailed deer removed from a 1.1 km^2 experimental removal area from 7 January to 27 February 2002 on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA.

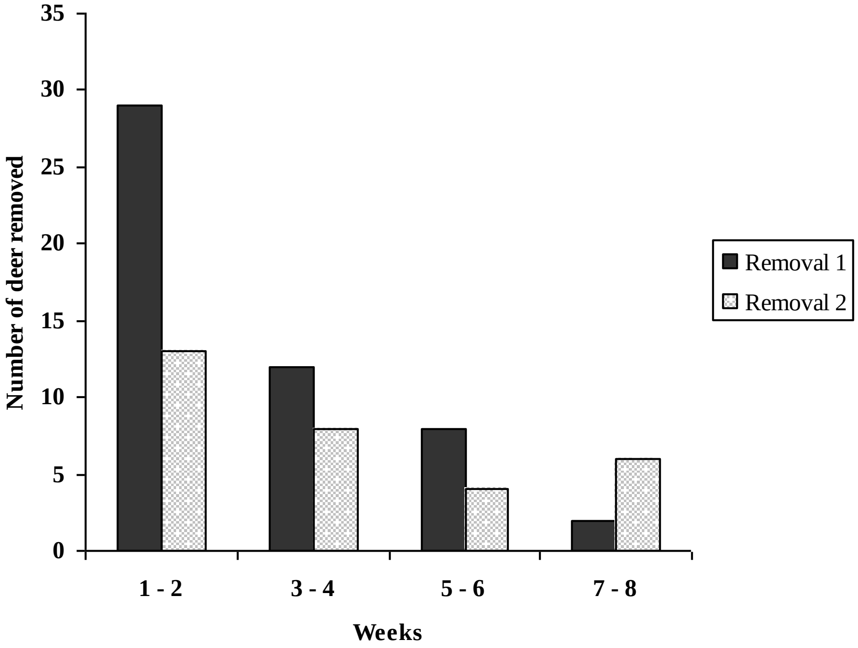

Fig. 4.4. The number of white-tailed deer removed from a 1.1 km^2 experimental removal area from 7 January to 27 February 2002 (Removal 1) and 1 January to 21 February 2005 (Removal 2) on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA.

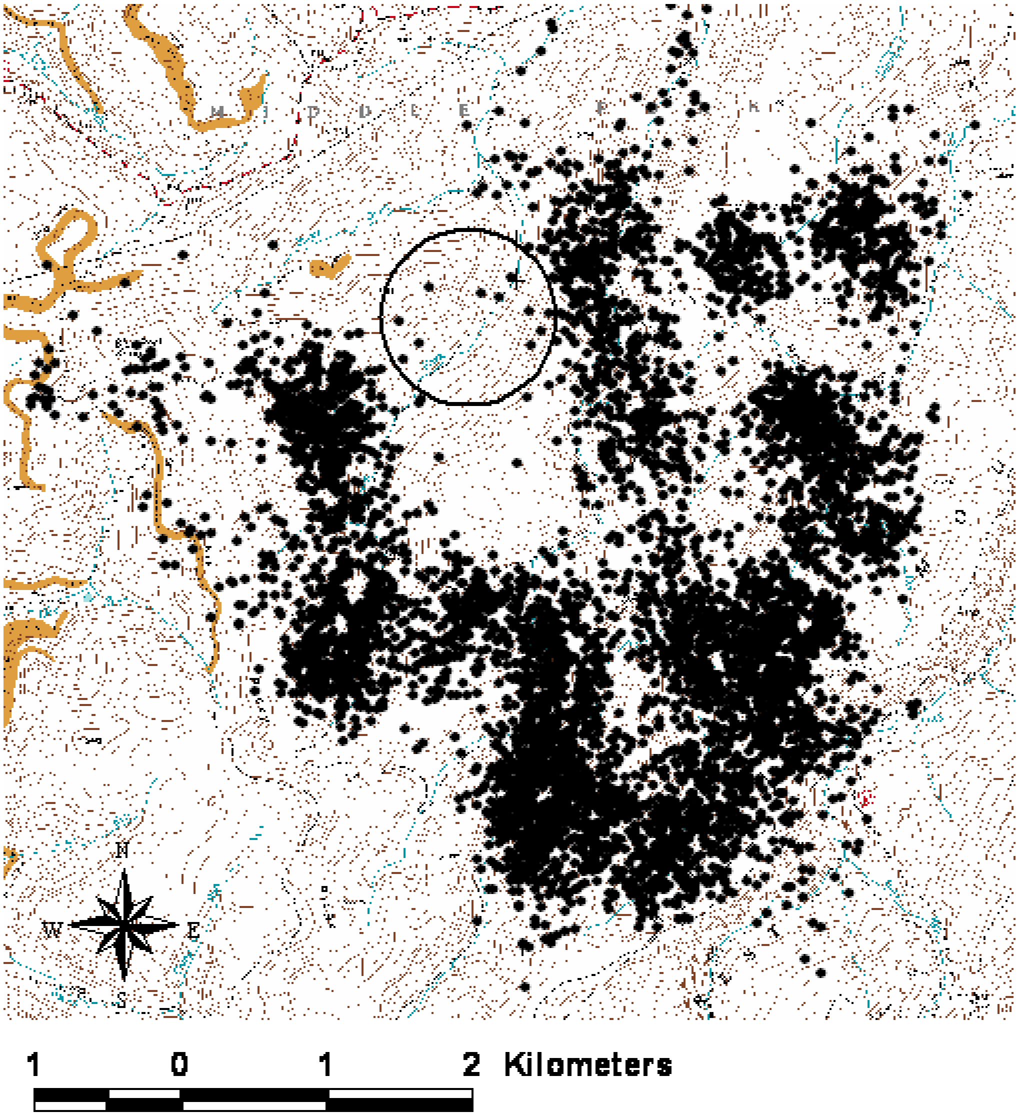

Fig. 4.5. Telemetry locations from 18 February 2002 to 20 December 2002 of 84 extant radiocollared deer (1 male and 83 female) after application of localized management on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA. The circular area represents the 1.1 km^2 removal area where the treatment was applied.

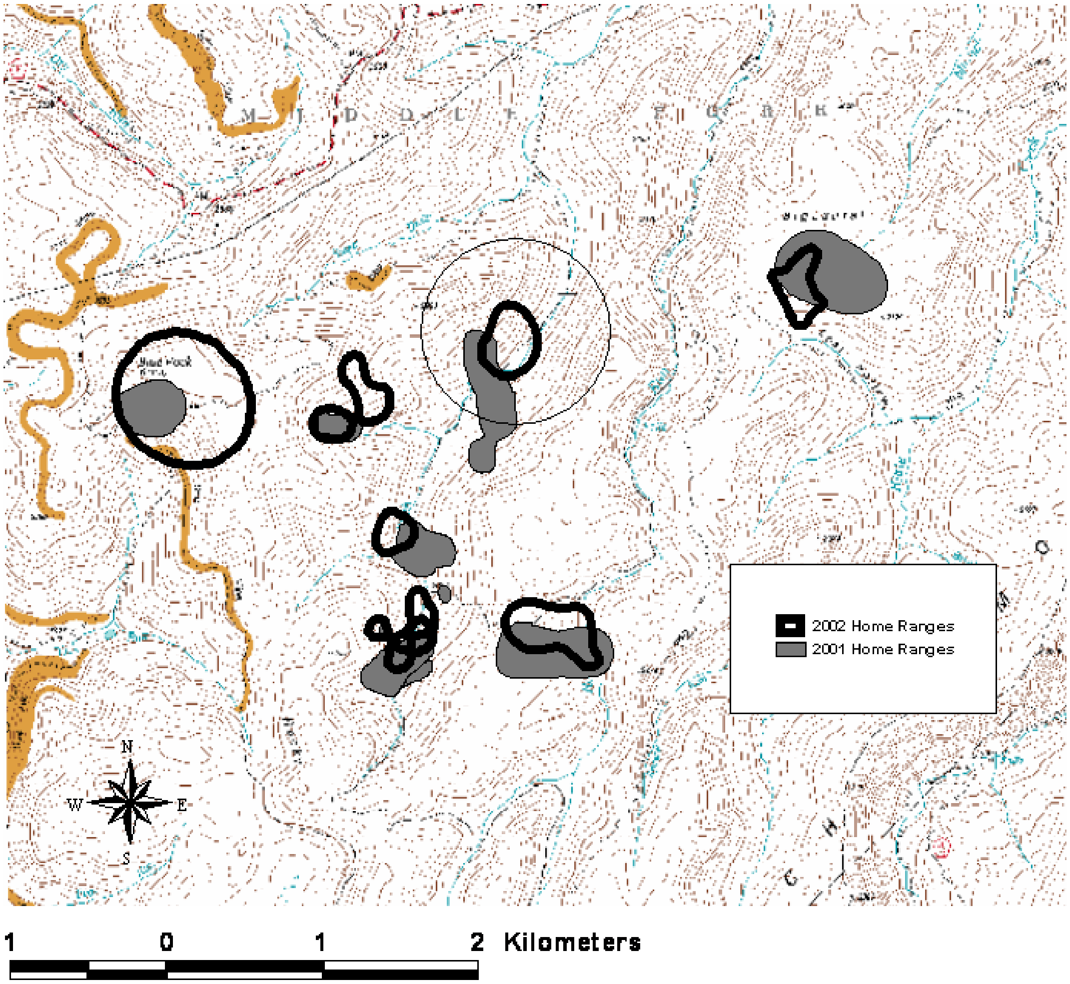

Fig. 4.6. The pre- and post-removal (2001 and 2002, respectively) summer home ranges (50% fixed kernel) of 8 adult female deer with significant home range shifts towards the removal after application of localized management on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA. The circular area represents the 1.1 km^2 removal area where the treatment was applied.

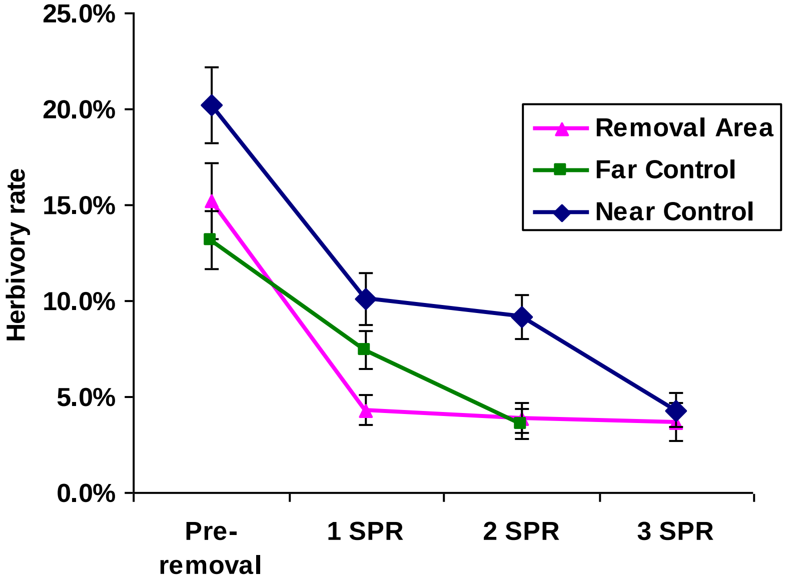

Fig. 4.7. Herbivory rates of regeneration sites pre-removal and 1–3 summers post removal (SPR) on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA from 2001–2004. Regeneration sites (n=6) were assigned to 1 of 3 categories (Removal Area, Near Control, and Far Control) for analysis.

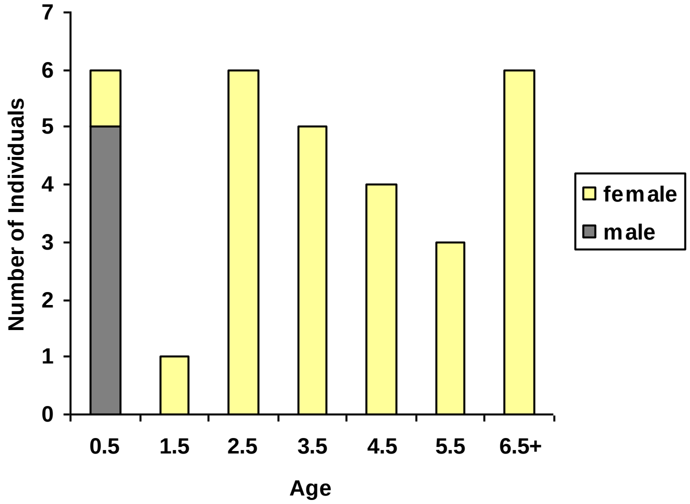

Fig. 4.8. Estimated ages of male and female white-tailed deer removed from a 1.1 km^2 experimental removal area from 1 January to 21 February 2005 on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, USA.

CHAPTER 5

POPULATION DIFFERENTIATION OF WHITE-TAILED DEER FOLLOWING AN APPLICATION OF LOCALIZED MANAGEMENT[1]

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[1] Miller, B. F., R. W. DeYoung, T. A. Campbell, B. R. Laseter, W. M. Ford, and K. V. Miller. To be submitted to the *Journal of Wildlife Management*.

Abstract: Localized management has been proposed as an alternative management technique for reducing conflicts of overabundant deer populations. The effectiveness of this technique depends on site fidelity and philopatry of adjacent females. To assess this, we compared the genetic relatedness of deer removed from a 1.1 km^2 removal area with deer collected three years later from the same removal area (i.e., repopulating animals). We found evidence of population differentiation based on significant Wright's F_{st}, Wright's F_{is}, and Hardy-Weinberg disequilibrium tests. Our evidence of repopulation by immigrant deer suggests that social behaviors of females in high density herds may not prevent repopulation of removal areas by surrounding animals.

Key words: genetics, F-statistics, localized management, microsatellites, *Odocoileus virginianus*, West Virginia, white-tailed deer.

INTRODUCTION

Localized management has been proposed as an alternative deer management technique that relies on the social organization of female white-tailed deer (*Odocoileus virginianus*) to reduce the negative social and ecological effects of overabundant deer populations. White-tailed deer social organization is structured as matriarchal social groups containing adult females and several generations of offspring inhabiting overlapping home ranges (Hawkins and Klimstra 1970, Hirth 1977, Mathews and Porter 1993). These social groups are formed as a result of infrequent (2-20%) dispersal of juvenile females, and philopatric home range formation of juvenile females (Mathews 1989, Tierson et al. 1995, Campbell et al. 2005). Social groups persist due to association of members throughout the year with the exception of the fawning season (Hawkins and Klimstra 1970).

Localized management proposes the "surgical" removal of a matriarchal social group(s) from a limited geographical area to create a 10–15 year period of reduced deer density (Porter et al. 1991). The persistence of the void depends on the encroachment of adjacent social groups, colonization by immigrant deer, and the number of animals surviving the removal efforts (Porter et al. 1991, McNulty et al. 1997, Oyer and Porter 2004, Miller 2008). This technique is intended to alleviate negative impacts of overabundant deer populations in specific areas rather than a more traditional widespread reduction in deer population density.

The first experimental application of the localized management was performed by McNulty et al. (1997) in the Adirondack Mountains on an unhunted, seasonally migratory, and low-density population. A subsequent investigation of the removal area indicated deer densities were reduced for a period of 5 years (Oyer and Porter 2004). Repopulating animals were offspring of animals surviving the removal efforts or immigrants from adjacent social groups (Oyer and Porter 2004). The results of that study suggest that localized management may be a viable alternative management technique where traditional approaches are unsuitable.

Still, it has been cautioned that behavioral plasticity may limit the universal applicability of behavior-based management techniques (Miller 1997, Comer et al. 2005). To investigate the utility of localized management in a situation representative of where deer-human conflicts occur, Miller (2008) conducted a test of this technique on a high-density deer population in the central Appalachian Mountains of West Virginia. That investigation reported that localized management provided only temporary, localized density reductions in high-density deer populations. However, the origin of repopulating animals within the removal area was not fully understood using traditional research techniques (e.g., radio-telemetry, visual observations, etc.).

The development of microsatellite DNA markers (Anderson et al. 2002) has allowed the generation of new information about the social behavior of white-tailed deer. Previous examinations of white-tailed deer ecology using molecular techniques have relied on allozyme markers (e.g., Mathews and Porter 1993, Scribner et al. 1997). However, use of microsatellite DNA loci allows increased precision for examining fine-scale genetic patterns (Anderson et al. 2002, DeYoung and Honeycutt 2005). Microsatellite data from white-tailed deer has been used successfully in paternity testing (DeYoung et al. 2002), investigations of spatial genetic structuring (Comer et al. 2005, Miller 2008), and assignment of individuals to specific populations (DeYoung et al. 2003). In this study, we used genetic markers to examine the origin of repopulating animals following Miller's (2008) application of localized management. Our objective was to compare the genetic relatedness of white-tailed deer removed during an application of localized management with animals collected three years later from the same removal area (i.e., repopulating animals) to help determine the origin of recolonizers. Secondarily, we sough to use these data to identify the possible limitations of the localized management technique.

STUDY AREA

Our study was conducted on the 3,413 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) located in Randolph County, West Virginia (38°42'N, 80°3'W). The MWWERF was located within the Unglaciated Alleghany Mountain and Plateau Physiographic province characterized by steep slopes and narrow valleys. Elevations ranged from 700 to 1,200 m and precipitation averaged between 170 and 190 cm/year primarily as snow fall. The forest cover type was predominantly an Allegheny hardwood-northern hardwood type (Keyser and Ford 2005). An investigation of the white-tailed deer population initiated in 1999 on the MWWERF indicated that the herd was characterized as a moderate to high density population with low female dispersal, high female survival, and male-biased hunting harvests. An extensive review of the study site and deer population is provided in Campbell (2003).

METHODS

We removed deer from a circular 1.1 km^2 area selected to encompass a targeted social group delineated from radio-telemetry, encompass two forest regeneration sites, and approximate the spatial scale of genetic variation previously determined (Laseter 2004). We captured deer via modified Clover traps (Clover 1954) baited with whole kernel corn from 7 January to 27 February 2002 (Removal 1). Intramuscular injections of succinylcholine chloride were administered to captured animals prior to euthanasia via a captive bolt gun upon recumbency. Periodic sharpshooting was conducted by West Virginia Department of Natural Resources personnel to remove trap-reluctant individuals after 4 weeks of trapping. Trapping data and observation of deer tracks in the snow were used to determine when to cease removal efforts. We conducted a second removal (Removal 2) from 1 January to 21 February 2005 utilizing the same trapping methods and duration as the initial removal. A detailed description of removal methods is available in Miller (2008).

Ear-notch tissue was collected from euthanized animals and placed in sterile glass tubes containing 8 ml of 95% ethanol, and allowed to fix at 4°C for ≥24 hours then stored at room temperature. Total DNA was extracted from tissue samples using Qiagen® DNeasy™ Blood and Tissue Kit (Qiagen, Inc., Valencia, California). Standard protocols were used except that we allowed 24 hrs for tissue lysis by proteinase K, and only 100µl of buffer AE was added to the membrane of the mini spin columns.

We selected a panel of 14 microsatellite loci from the 21 identified for use in white-tailed deer (Anderson et al. 2002). The BM145, BM203, BovPRL, ETH152, K, OCAM, and R loci were omitted. DNA fragments were amplified by polymerase chain reaction (PCR) following methods by Anderson et al. (2002) and subjected to capillary electrophoresis on an ABI PRISM® 3130 Genetic Analyzer (Applied Biosystems, Foster City, California). Alleles were characterized by GeneMapper™ software (Applied Biosystems) followed by visual inspection and verification.

To compare genetic characteristics of the Removal 1 population with the Removal 2 population we calculated gene diversity (Nei 1987), allelic richness (El Mousadik and Petit 1996), and number of alleles. We tested for deviations from Hardy-Weinberg equilibrium for each population at each locus and overall by permuting alleles among individuals 280 times within samples. Significance testing was corrected for multiple comparisons using the sequential Bonferroni technique (Rice 1989). An overall Wright's F_{is} value was calculated for each population after 560 randomizations of alleles. Population differentiation was examined using Wright's (1951, 1969) F_{st} according to the methods of Weir and Cockerham (1984). Standard errors were estimated by jackknifing across loci, and significance was confirmed by permuting genotypes across samples 20 times. To assess if the differentiation between the 2 populations was biologically based and not an artifact of sample size disparity, we arbitrarily divided the Removal 1 population into 2 samples and estimated F_{st} as before. All analyses were conducted using the computer program FSTAT ver. 2.9.3 (Goudet 1995).

RESULTS

During Removal 1, we removed 51 deer ranging in ages from 0.5-8.5+ years. Females comprised the majority of the animals (39 of 51), with a mean (± SE) age of 3.7±0.4 years (range = 0.5–8.5+ years old). The mean age was lower for males (0.9±0.3 years old) because most males were fawns (9 of 12). Male ages ranged from 0.5–3.5 years old. Genetic samples were not obtained from 3 females collected during the removal efforts resulting in a final sample of 48 individual genotypes. Based on track counts in the snow and radio-monitored animals (n=9), >80% of the deer population was removed.

During Removal 2 we collected 31 deer ranging in ages from 0.5–8.5+ years using the same techniques and trapping duration as Removal 1. Females again comprised the majority of the animals removed (26 of 31). The mean age of females was 4.5 ± 0.5 years (range = 0.5–8.5+). Eighteen of the females were ≥3.5 years of age. All 5 males removed were fawns (0.5 years). The genetic data of 1 additional 2.5 year old female collected approximately 3 weeks after the cessation of the Removal 2 trapping period by West Virginia Department of Natural Resources personnel was included in the analysis resulting in a final sample size of 32 individual genotypes.

Estimates of within-population genetic diversity indicated that the 14 microsatellite loci examined were highly polymorphic (Table 5.1). A total of 162 unique alleles were observed between the Removal 1 and Removal 2 populations. The number of alleles per locus ranged from 3–18 for the two populations. Allelic richness per locus ranged from 3.0–14.7 and 3.7–15.5 for the Removal 1 and Removal 2 populations, respectively. Gene diversity ranged from 0.39–0.92 and 0.43–0.92 for the Removal 1 and Removal 2 populations, respectively.

Locus specific Hardy-Weinberg equilibrium tests detected deviation in 1 locus (BM848) for the Removal 1 population. No locus specific departures from Hardy-Weinberg were detected in the Removal 2 population. A slight overall departure ($P=0.05$) from Hardy-Weinberg equilibrium was detected for the Removal 1 population, however no overall departure ($P=0.318$) was detected for the Removal 2 population.

The overall Wright's F_{is} value was statistically significant in the Removal 1 population ($F_{is}=0.031$, $P=0.037$), but not in the Removal 2 population ($F_{is}=0.009$, $P=0.339$). A low but statistically significant ($P<0.05$) Wright's F_{st} value was detected between the 2 populations ($F_{st}=0.011$, $SE=0.005$). Subsequent F_{st} analysis of the Removal 1 population after arbitrary division detected no difference from 0.0 ($F_{st=}0.005$, $SE=0.004$). The test for differentiation also detected no difference between the populations ($P=0.25$) and discounts sample size disparity as a source of statistical significance.

DISCUSSION

Mathews (1989) reported that female social groups in the central Adirondack Mountains of New York were composed of an older female whose home range was overlapped by several generations of female offspring forming a social unit similar in shape to the petals of a rose. A subsequent genetic examination of social groups on that study site (Mathews and Porter 1993) confirmed the presence of genetic structure at the level of a social group attributed to female philopatry.

In contrast, Comer et al. (2005) found only limited evidence for spatial genetic structuring in a population of white-tailed deer in the Upper Coastal Plain of South Carolina. A history of intensive harvests and young age structure among does may have limited the formation of persistent, cohesive social groups. They concluded that exploited populations do not expand by the addition of outwardly radiating home ranges of new offspring as predicted by the rose petal hypothesis. Rather, some populations may expand similarly to the “gas diffusion” population expansion model, where deer move from high-density areas to lower-density areas (Porter et al. 1991).

The preliminary examination of the spatial genetic structure of the white-tailed deer on our study site confirmed that genetic relatedness was inversely related to the geographic distances between individuals (Miller 2008). We also attributed those findings to spatial fidelity of matrilineal social groups resulting from philopatric female offspring in accordance with the rose petal hypothesis. Therefore, the study site met the requirement of localized management that assumes spatial genetic structure of female white-tailed deer due to philopatry and low dispersal.

The results from our current investigation of the genetic relatedness within the Removal 1 population provide additional evidence of spatial genetic structuring. The Hardy-Weinberg equilibrium test performed detected a slight heterozygote deficiency in the Removal 1 populations. Anderson et al. (2002) reported that deviations from Hardy-Weinberg equilibrium can be attributed sampling of related individuals. Furthermore the Wright’s F_{is} test was significant in the Removal 1 population indicating some degree of inbreeding due to philopatric behaviors of related females. Therefore, we expected that population expansion after the application of localized management would occur in accordance with the predictions of the rose-petal hypothesis. Oyer and Porter (2004) reported that none of the repopulating animals in a $1.4km^2$ removal area implemented by McNulty et al. (1997) were likely dispersers from distant areas. Rather, they concluded that the repopulating animals originated from the removal area or areas immediately adjacent to it.

In contrast, the genetic evaluation of our Removal 2 population detected no evidence to support the prediction that repopulating animals originated from within the removal area. No single locus or population-wide deviations from Hardy Weinberg equilibrium were detected, and no inbreeding was detected by F_{is} testing. The decrease in F_{is} of the Removal 2 population is consistent with immigration of unrelated deer into the removal area. Additionally, Wright's F_{st} test of the Removal 1 and Removal 2 populations was significant, indicating differences in allele frequencies. Thus, repopulating deer were not individuals that survived removal efforts, but rather were unrelated animals with dissimilar genetic characteristics. Of the 32 deer in the Removal 2 population, 18 of them were alive at the time of the initial removal based on age estimations (Severinghaus 1949). It is unlikely that all of these animals survived the initial removal efforts, which provides further evidence of immigration into the area by unrelated animals. Therefore, we conclude that repopulation of the removal area did not occur by reproduction of missed animals as in the Adirondack studies (Oyer and Porter 2004). Instead the rapid colonization of the removal area suggests an influx of females from the surrounding landscape.

Site fidelity of female offspring is initially advantageous to both the mother and her young. The maternal investment increases the chance of survival of offspring and its future reproductive potential (Trivers 1974). However, mothers would be expected to decrease their investment as offspring mature, and expending resources on additional young becomes ultimately more beneficial. Hawkins and Klimstra (1970) reported that 82% of doe pairs have separated socially by the time the younger member reaches 3 years of age. Furthermore Nelson and Mech (1984) found that after 3 years of age, social interactions and paired migration ceased between a mother and daughter.

As younger or subordinate females leave social groups to become the matriarch of their own group, the benefits of spatial fidelity must outweigh the costs. Spatial fidelity increases the relatedness of individuals in a geographical area; however, it also increases competition for resources (Gardner and West 2006). Disadvantages to dispersal of maturing females include energy diversion for home range exploration and searching, and conflicts with previously established matrilineal groups (Nelson and Mech 1984). A study by Ozoga et al. (1982) reported in dense populations, subordinate females dispersing from ancestral ranges were relegated to unsuitable fawning grounds or into buffer zones between boundaries of contiguous territories controlled by dominant matriarchs. However, after a drastic population reduction was implemented around a family group, subordinate females established fawning territories in peripheral unoccupied ranges that were previously unavailable because of aggressive defense by neighboring females of higher social rank. Additionally, Storz et al. (1999) speculated that newly established mammalian social groups may be more likely to colonize unoccupied peripheral environments when dispersing. Therefore, unoccupied peripheral areas with reduced intrasexual and intraspecific competition may be viewed more favorably than their original home range, especially in high-density populations.

MANAGEMENT IMPLICATIONS

The foundation of the localized management concept is that populations expand slowly into new areas because of the social organization of female white-tailed deer. However, our results suggest a single application of localized management in high-density deer herds may only provide temporary reductions of deer-densities. Our evidence of population differentiation suggests that social behaviors of females may not prevent repopulation of removal areas by surrounding animals. Females forming new matrilineal groups may select areas with abundant resources (e.g., timber harvests) and reduced competition, thus limiting the persistence of the void. In high-density deer populations we recommend either repeated deer removals of every 2–3 years on localized sites, or larger landscape-level decreases of deer density to prevent the negative effects of overabundant deer.

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Table 5.1. Sample size (n), total number of alleles, number of private alleles, mean genetic diversity (range), mean allelic richness (range), number of loci out of Hardy-Weinberg equilibrium, and Wright's F_{is} value for 14 microsatellite loci in 2 populations of white-tailed deer sampled in the winter of 2002 (Removal 1) and 2005 (Removal 2) in Randolph County, West Virginia, USA.

Pop	n	# alleles	# private alleles	gene diversity (range)	allelic richness (range)	HWE	Fis
Removal 1	48	144	18	0.79 (0.39-0.92)	9.1 (3.0-14.7)	1/14	0.031*
Removal 2	32	132	24	0.77 (0.43-0.92)	9.2 (3.7-15.5)	0/14	0.009

* Statistically significant $P \leq 0.05$

CHAPTER 6

CONCLUSIONS

My results represent the culmination of research investigating white-tailed deer and forest ecology on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) in Randolph County, West Virginia. Research efforts investigating the ecology of white-tailed deer on the MWWERF began in 1999. Results indicated that the deer population was at a high-density (Langdon 2001) and characterized by moderate fawn recruitment, excessive harvest of yearling males, and conservative harvest of females (Campbell 2003). Additionally, Campbell (2003) concluded that female philopatry was high and dispersal rates were low. Subsequent examination of spatial and genetic structure of the deer population by Laseter (2004) confirmed the presence of spatial and genetic structure in the population consistent with matrilineal groupings of white-tailed deer. It was concluded by both Laseter (2004) and Campbell (2003) that the rose-petal model of population expansion proposed by Mathews (1989) applied to the deer population on the MWWERF and that a test of localized management would be prudent. However, Laseter (2004) cautioned that the high population density forced overlap among matriarchal groups, and that the effectiveness of behavior-based management strategies may be affected.

Utilizing information obtained in the previous research efforts, my investigation focused on the effects of deer herbivory on forest regeneration, alternative techniques to mitigate deer herbivory, and white-tailed deer spatial genetic and sociobiological characteristics. My results indicate that the high deer-densities on the MWWERF may be impacting forest regeneration and ecosystem processes. Although natural woody vegetation was able to outgrow competing herbaceous vegetation, preferential herbivory by white-tailed deer can affect woody species of limited availability. The declines in herbivory rates after increased timber harvesting on the study site suggests that providing abundant browse through forest management may be a viable alternate management technique for mitigating impacts of overabundant deer populations.

My analysis of genetic and social structuring documented strong evidence of microgeographic (<1 km) spatial structuring in the population, which was attributable to spatial fidelity of matriarchal social groups. However, the application of localized management only provided a temporary reduction in deer densities despite fulfilling *a priori* socio-behavioral requirements. Genetic analysis of repopulating animals indicated they were genetically different from animals removed during the initial removal effort, suggesting that social behaviors of adjacent females may not prevent repopulation of removal areas by surrounding animals. It appears that in high-density deer populations, larger landscape-level deer removals or repeated deer removals (e.g., 2–3 years) may be more effective than localized management in preventing the negative effects of overabundant deer.

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