AN ANALYSIS OF SPATIAL AND GENETIC POPULATION STRUCTURE IN WHITE-TAILED DEER WITH IMPLICATIONS FOR MANAGEMENT

by

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(Under the Direction of Karl V. Miller)

ABSTRACT

Recently proposed models describing white-tailed deer (*Odocoileus virginianus*) social ecology have been used as the basis for management strategies. Population expansion models describe the formation of persistent matrilineal social groups among female deer, with limited dispersal of young females. The localized management concept proposes that removal of social groups will produce persistent areas of reduced deer density due to social restrictions on colonization of new habitats by females. However, this species exhibits a remarkable degree of behavioral plasticity in response to varying conditions and the social behaviors underlying localized management have been tested only in a limited range of habitats and locations. I evaluated the potential for localized management to reduce the incidence of deer-vehicle collisions in a low density, intensively managed deer population on the Savannah River Site (SRS) in the upper Coastal Plain of South Carolina. Based on radiotelemetry data collected for 17 female deer in combination with genotype data for 38 females at 14 microsatellite DNA loci, I determined that female deer at the SRS did not form the cohesive, persistent social groups described by the population expansion models. Dispersal rates of female deer also appeared greater than rates reported in other populations. I used microsatellite DNA analysis of nearly

400 individuals to show that deer at the SRS exhibited little genetic structure across the 800-km^2 study site, in contrast to previous investigations showing genetic structure at state or regional scales. Tests of dispersal also suggested high rates of female-mediated gene flow. I also conducted a field test of the localized management concept by implementing removal actions in 4 corridors surrounding major roadways. Genetic analyses indicated that, in contrast to previous tests of the concept, removal corridors did not form genetically distinct subpopulations. The removal actions were effective in reducing population density in the road corridors in the short term; however, the persistence of these reductions is uncertain. Management history, especially the high doe harvest, of the SRS population provided a logical explanation for my observations. Overall, the results of the study do not support the universal applicability of the studied models of deer social ecology and of the localized management concept.

INDEX WORDS: Localized management, Microsatellites, *Odocoileus virginianus*, Population genetics, Radiotelemetry, Savannah River Site, South Carolina, White-tailed deer

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

The white-tailed deer (*Odocoileus virginianus*) is among the most economically important and controversial species of wildlife in North America. Economically, this species is valued both as the most popular big-game animal for hunters in the United States and as the subject of nonconsumptive uses such as wildlife watching and photography. An analysis conducted by Williamson and Doster (1981) estimated the total annual value of the nation's white-tailed deer herd at $8.2 billion. This number included approximately $2.8 billion in values for hunters and $5.4 billion in values to nonhunters. The deer herd has increased rapidly since 1981, so the value of the current herd is likely to be considerably higher. Conover (1997) estimated the recreational benefits of white-tailed deer at more than $14 billion per year.

White-tailed deer have undergone a massive population increase since reaching an historic low of approximately 350,000 animals around 1900 (McCabe and McCabe 1984). Estimates in 1993 placed the nationwide population at approximately 26 million animals (Jacobson and Kroll 1994). Indeed, in many areas of the country deer have reached population levels that have negative impacts on society. These negative impacts include damage to agricultural crops and landscape plantings, changes in plant community composition and structure (e.g., McShea and Rappole 1997), regeneration failures of commercially harvested timber stands (Alverson et al.

1988; Tilghman 1989), and deer-vehicle collisions. Conover (1997) estimated negative impacts from deer at greater than $2 billion per year.

The largest component of the negative impacts estimated by Conover (1997) was approximately $1 billion in damages to automobiles from deer-vehicle collisions. Numbers of deer-vehicle collisions are increasing in most states, with a conservative estimate of 500,000 accidents in 1991 (Romin and Bissonette 1996). Collisions between deer and vehicles result in property damage and can cause human injuries or death. Data from Michigan (Hansen 1983) and Ohio (Stoll et al. 1985) indicated that 4-5% of deer-vehicle collisions resulted in human injury. Assuming these are representative of deer-vehicle accidents in general, this would suggest that annually up to 25,000 people are injured in deer-vehicle collisions nationwide. Although precise estimates of the monetary cost of deer-vehicle collisions vary (Schwabe and Schuhmann 2002), there can be little doubt that the issue is a significant, and growing, problem facing wildlife managers (Romin and Bissonette 1996).

The most effective and commonly used method to reduce deer-vehicle collisions and other negative impacts is population control or reduction. Recreational hunting is the primary means by which deer populations have traditionally been controlled; however, recreational hunting may not be acceptable in some areas due to safety or societal concerns. Application of alternative lethal control measures, like sharpshooting or trap and euthanize programs, over large areas can be expensive and time-consuming (Doerr et al. 2001). In addition to population reduction, other strategies proposed to reduce deer-vehicle collisions have included lighted signs (Pojar et al. 1975), warning whistles (Romin and Dalton 1992), highway fences (Falk et al. 1978), crosswalks (Lehnert and Bissonette 1997), and highway reflectors (Reeve and Anderson 1993). In general, these technologies have met with limited success due to ineffectiveness or cost efficiency.

With increasing management concerns over negative impacts from white-tailed deer, strategies have been proposed to more effectively manage deer populations in limited areas (Porter et al. 1991). These strategies are based on assumptions about deer social behavior and hold promise for management of deer in suburban and forested habitats (Porter et al. 2004, Campbell et al. 2005). However, white-tailed deer exhibit plasticity in their social behavior in response to different habitats and other factors (Marchinton and Atkeson 1985). Before management strategies that rely on social behavior are applied universally, the implications of behavioral plasticity for the effectiveness of these strategies should be determined (Miller 1997). This study examines the potential effectiveness of behavior-based management strategies in a low-density white-tailed deer herd in South Carolina. I examined this problem both in terms of the validity of the underlying assumptions and in terms of the potential applicability of these strategies to the issue of deer-vehicle collisions.

LITERATURE REVIEW

Social Structure and Behavior

White-tailed deer social organization in most habitats consists of a simple dominance hierarchy, with two important, gender-based social groupings (Miller et al. 2003). Male and female groupings are typically isolated during the nonbreeding season (McCullough et al. 1989). Among females, studies have shown that individuals form persistent matriarchal groups that include an older doe, her offspring of the year, and often female offspring from previous years (Hawkins and Klimstra 1970, Aycrigg and Porter 1997). Dominance status among does is primarily a function of age (Hirth 1977). In the fawning season, does isolate themselves before parturition and will actively defend a fawning territory from other deer (Ozoga et al. 1982). Female social groups re-form approximately 8–10 weeks after parturition. In some northern habitats, matriarchal groups may fuse in the fall and winter to make predictable seasonal migrations between summer and winter range (Tierson et al.1985, Nelson 1998). Large winter aggregations may function as independent subpopulations or demes (Nelson and Mech 1987).

In contrast to the relatively stable social structure among females, male white-tailed deer form loosely knit bachelor groups during the nonbreeding season. Male groupings do not generally consist of related individuals and group membership changes over time (Miller et al. 2003). Bucks form dominance hierarchies based primarily on physical size and maintained by dominance displays and threatening postures (Hirth 1977). During the nonbreeding season, social relationships among bucks can be amiable but male social groupings break up near the onset of breeding. In herds where older males are present, the predominant view has been that breeding opportunities are limited to a few, dominant males (Miller et al. 2003).

Studies of dispersal in white-tailed deer have generally shown higher dispersal in young males and greater philopatry in females. Dispersal of females was low (<5%) in radiotelemetry or mark-recapture studies in Georgia (Kammermeyer and Marchinton 1976), Montana (Dusek et al. 1989), New York (Aycrigg and Porter 1997), and West Virginia (Campbell et al. 2005). Dispersal rates in these habitats apparently were not dependent on population density (Porter et al. 1991). However, variation in dispersal rates of female deer has been observed. In an intensively farmed region of Illinois, Nixon et al. (1991) observed >40% dispersal of young does, and dispersal rates of 15-20% have been found in Minnesota (Nelson and Mech 1992, Nelson 1993) and Nebraska (VerCauteren 1998). In contrast, young male deer typically disperse at a higher rate, possibly in response to aggression from their dam or other related females (Holzenbein and Marchinton 1992). Highest rates of dispersal in both sexes are in the fawn and yearling age classes.

Genetic Structure

Many species exhibit spatial genetic structuring because of limitations in gene flow among populations. Gene flow tends to homogenize populations, but geographic barriers to migration or isolation by distance can prevent gene flow and result in local adaptation, differentiation, and eventually speciation (Slatkin 1987). Understanding gene flow and population structure is important in basic population ecology for any species and it has implications for conservation biology and wildlife population management (Balloux and Lugon-Moulin 2002). Genetically isolated populations may show reduced heterozygosity and allelic richness, with potentially negative effects on fitness and long-term viability (Nei et al. 1975, Luikart and Cornuet 1998). In the case of abundant species or game species, knowledge of population structure and gene flow can affect management strategies (Porter et al. 1991, Cegelski et al. 2003).

Several studies have used allozyme and restriction enzyme analysis to examine population genetics of white-tailed deer on state or regional scales. In a study of 29 locations in Tennessee, Kennedy et al. (1987) found that both geographic location and herd origin (i.e., stocking source) were associated with genetic differences between populations although geographic proximity was a better predictor of genetic similarity. Ellsworth et al. (1994) and Leberg et al. (1994) used both mitochondrial DNA restriction enzyme analysis and allozymes to examine the influence of stocking history on white-tailed deer populations in the Southeast. Their results suggest that historic stocking efforts could have substantial and persistent effects on the genetics of local populations near the site of release (Leberg and Ellsworth 1999). However, limited dispersal of deer has apparently prevented widespread influence of stocked populations in areas not directly subject to stocking efforts (Leberg and Ellsworth 1999).

Based on a comparison of maternally inherited mitochondrial DNA and biparentally inherited allozymes for deer from South Carolina and Georgia, Purdue et al. (2000) found significant genetic structure at a regional scale. They concluded that males dispersed more than females in the Southeast and that females rarely dispersed greater than 50 km. A more recent study by DeYoung et al. (2003a) using microsatellite DNA markers found significant differentiation at the state level of deer populations in Mississippi. They also found evidence that stocking history influenced current genetic characteristics of the populations. Fewer studies have examined genetic structure at smaller spatial scales, but Ramsey et al. (1979) reported that two adjacent populations in South Carolina differed in characteristics at several allozyme loci. Scribner et al. (1997) found significant nonrandom clustering for several loci in the same herd. In New York, Mathews and Porter (1993) suggested that female matriarchal groups formed genetically distinct units at the local scale.

Localized Management and the Rose Petal Hypothesis

Localized management of deer is a concept that may hold potential for reducing deer-vehicle collisions around heavily traveled roads. This concept proposes that persistent areas of low deer density can be maintained by locally removing entire social groups of deer (Porter et al. 1991). This concept is based on two assumptions regarding the social organization of white-tailed deer: female deer are highly philopatric (they remain in their natal range for life) and female offspring occupy home ranges close or adjacent to their mothers. These factors imply that female deer will only slowly occupy areas of habitat where deer have been removed by management actions.

The concept of localized management was developed from a 30-year series of studies conducted on a population of white-tailed deer in the Adirondack Mountains of New York. Using individually marked and radiocollared deer, Tierson et al. (1985) identified several “social groups" of female deer that occupied similar geographic range and made similar seasonal movements (e.g., between summer and winter range). Female deer exhibited high range fidelity over the 8-year study period, with approximately 4% (9 out of 240 does) dispersing.

Mathews and Porter (1993) found that genetic structure existed in the deer herd at the level of the social group; that is, the social groups consisted of related animals. Female offspring generally formed home ranges that at least partially overlapped that of their dams. Based on these data, Porter et al. (1991) proposed a hypothetical model for deer population expansion. According to this model, the female component of the population expands in space as a series of overlapping home ranges that are similar to the petals of a rose. The social group thus forms a rose shape, with the oldest doe occupying the center of the rose and younger individuals occupying home ranges nearer the periphery. As new females are born, they establish home ranges overlapping existing ranges on the outer limits of the social group. This model is termed the "rose-petal expansion model" (Porter et al. 1991) and it contrasts with the traditional gas diffusion model of population expansion, whereby deer rapidly relocate from areas of higher density to unoccupied habitat in a manner similar to gas molecules reaching equilibrium in space.

If the rose-petal expansion model accurately represents deer behavior, then it would be possible to maintain persistent, localized areas of low deer density for long periods of time (up to 15 years; Porter et al. 1991). If an entire social group were removed from an area, recolonization could take place either by encroachment from adjacent social groups or by a long-distance dispersal. In the first case, the gradual encroachment by adjacent groups (i.e., adjacent roses) is likely to take considerable time as each generation forms new home ranges that overlap existing home ranges. Because dispersal (and therefore colonization) by females is presumed to be rare, recolonization by this mechanism is unlikely.

For management purposes, the rose petal hypothesis suggests that by applying intensive removal to areas of concern, an area of low density can be created that will persist for an extended time period. This management strategy is referred to as localized management (McNulty et al. 1997). The amount of effort required is likely to be smaller than that needed to reduce general population density over a larger area. McNulty et al. (1997) conducted a limited test of localized management in the Adirondacks population. They removed a social group of 14 does and then observed the movements of deer in adjacent social groups using radiotelemetry. After the removal, a local reduction in deer density was observed; however, deer in adjacent social groups did not significantly alter their home ranges in response to the removal. Oyer and Porter (2004) examined the same removal area approximately 6 years post-removal and found that radiocollared deer from adjacent habitats did not move into the removal area in that time. Although deer density in the entire research area declined markedly during the 6-year period, abundance within the removal area remained reduced relative to surrounding habitats (Oyer and Porter 2004).

The implications of localized management for deer managers are far-reaching and timely. By selectively removing groups of related deer along heavily traveled roadways, zones of low deer density could be created and maintained along these roadways. Thus, deer-vehicle collisions would presumably be reduced without the effort required to reduce general deer population density over wider areas. In addition to applications for reducing deer-vehicle collisions, this strategy could apply to other situations where a relatively small area of high deer density causes problems. Examples include suburban developments, small parks, and regenerating timber stands (Porter et al. 2004).

Applicability of Localized Management

The localized management concept is an appealing strategy for wildlife managers concerned about negative impacts from white-tailed deer over limited spatial areas. Indeed, it has been widely proposed for management of deer populations in suburban and urban habitats (Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004) and in the vicinity of timber regeneration areas (Campbell et al. 2005, Oyer and Porter 2004). In many cases, localized management is recommended with little information on social behavior or structure in the managed population, or with limited data regarding adult range fidelity only. True tests of the effectiveness of the localized management concept are limited to the single removal experiment conducted in the Adirondack Mountains (McNulty et al. 1997, Oyer and Porter 2004).

White-tailed deer exhibit remarkable plasticity in their social behavior depending on habitat and geographic area (Marchinton and Atkeson 1985). For example, in northern temperate areas of the United States, deer exhibit a well defined fall breeding period or "rut" when the majority of females come into estrous synchronously and are bred. In tropical latitudes, breeding occurs year-round (Demarais et al. 2000). Northern deer also make seasonal migrations from winter to summer range and may exhibit yarding behavior during severe winters. Deer in milder climates do not typically make regular seasonal movements. The primary social organization in forested or mixed habitats is solitary animals or small, single-sex groups but deer in open habitats may associate in larger, mixed herds (Hirth 1977). Female dispersal rates can vary widely depending on habitat conditions (Nixon et al. 1991, Porter et al. 1991). Given this evident plasticity, it seems prudent to examine the localized management concept and the underlying population model in a variety of conditions prior to widespread application.

Genetic Applications

The use of molecular techniques to address problems in management or conservation of wildlife is becoming more widespread. Molecular approaches have been used to estimate genetic variation and phylogenetic relationships among populations or species, examine the consequences of habitat and range fragmentation, and examine evolutionary significance of various traits (Honeycutt 2000). Of particular interest for this study is the use of population genetics analysis in combination with behavioral and demographic information to address hypotheses about population structure, gene flow, and breeding behavior. With the development of more variable markers such as microsatellite DNA loci, these techniques can be used to examine population parameters at a variety of spatial scales.

Microsatellites are tandemly repeated sequences of DNA with a unit of repetition between one and five base pairs (Jarne and Lagoda 1996). The most common and most useful types of microsatellites are di-, tri, and tetranucleotide repeats. The CA/TG dinucleotide repeat is the most common repeat in the mammalian genome (Hancock 1999). Microsatellite loci are distributed roughly randomly over the genome of most eukaryotic organisms (Hancock 1999). The functional significance of microsatellite sequences in the eukaryotic genome is uncertain, although there is some evidence that they are involved in cellular function (Kashi and Soller 1999). Microsatellites have been used in many applications, including gene mapping, genetic forensic analysis, microevolutionary studies, and relatedness studies.

Of immediate concern for population geneticists is the fact that microsatellite regions have exceptionally high mutation rates (Jarne and Lagoda 1996). This makes them useful for studies examining short evolutionary time frames or small spatial scales. Furthermore, the predominant mutation mechanism in microsatellites is by DNA polymerase replication slippage (Hancock 1999). This implies that during DNA replication, the polymerase misaligns the original and replicated strands such that one or more units of the repeated sequence are looped out. The consequence is that different alleles at a given locus vary in length by some multiple of the size of the repeated motif. That is, alleles of a tetranucleotide repeat will vary by some multiple of four base pairs. Thus, different alleles at a locus are recognizable as discrete size variants (Blouin et al. 1996). Microsatellite alleles, therefore, can be identified by amplifying the appropriate region by polymerase chain reaction and performing gel electrophoresis to separate alleles by size (Weber and May 1989).

Blouin et al. (1996) showed that microsatellites could accurately determine relatedness in mice. By using a battery of 21 microsatellite loci, they were able to correctly identify full siblings nearly perfectly and identify half siblings approximately 80% of the time. More polymorphic loci provided much greater power in discriminating related individuals. Additional discriminatory power and accuracy was provided by including additional loci and by including more polymorphic loci. Microsatellites have been used successfully to address a wide range of hypotheses regarding population and social structure, including determining relatedness of individuals between and within populations (Blouin 2003), parentage analysis (Marshall et al. 1998), analyzing differentiation of subpopulations (Balloux and Lougon-Moulin 2002), assigning individuals to populations (Paetkau et al 1995), and determining sex-biases in dispersal (Goudet et al. 2002).

The development of a panel of 21 microsatellite DNA loci for white-tailed deer (Anderson et al. 2002) provides an opportunity to use molecular approaches to look at fine-scale and landscape-scale population structure in this species. Among the Cervidae, microsatellites have been developed and applied to examine population structure in sika deer (*Cervus nippon*, Goodman et al. 2001), roe deer (*Capreolus capreolus*, Wang and Schreiber 2001) reindeer (*Rangifer tarandus*, Cote et al. 2002), and moose (*Alces alces*, Broders et al. 1999). DeYoung et al. (2003a, 2003b) evaluated the loci developed by Anderson et al. (2002) for white-tailed deer and found them to be useful for population differentiation, population assignment, and parentage analysis.

The Savannah River Site

We conducted this research at the Savannah River Site (SRS), an approximately 800-km^2 National Environmental Research Park encompassing portions of Aiken, Barnwell, and Allendale Counties in South Carolina. The SRS is administered by the U.S. Department of Energy (DOE) and managed jointly by DOE and Westinghouse, Inc. While active facilities occupy portions of the site, most of the SRS is undeveloped. The SRS is approximately 68% pine forest and consists primarily of variable-aged stands of longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine (Imm and McLeod in press). Swamps and riparian bottomlands dominated by hardwoods, including oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and blackgum (*Nyssa sylvatica*), occupy 22% of the site. Upland hardwoods, including oaks and hickories (*Carya* spp.), represent approximately 7% of land cover. Forested stands are interspersed with open habitats such as powerline rights-of-way, recent timber harvests, and road/facilities areas. The SRS is within the upper Coastal Plain physiographic province.

The deer herd at SRS has been managed since 1965 by annual dog-drive deer hunts over much of the site. Management sets annual removal goals to maintain a sitewide population of 4,000 animals (5/km^2) to minimize deer-vehicle collisions while maintaining a healthy population (Johns and Kilgo in press). Standard management hunts are large-scale dog drives, covering more than 25 km^2 and involving >70 dog packs (with 2 handlers each) and 100-200 stationary stand hunters. Between 1990 and 2000, annual hunts removed 1,000–1,700 deer from the site (Johns and Kilgo in press). Current population density varies across the site but is generally estimated at 4-6 deer/km^2 in most areas (Johns and Kilgo in press). Despite the low deer density, deer-vehicle collisions on site roads are considered a management problem. From 1990–2000, the SRS averaged approximately 75 deer-vehicle collisions annually, and data indicate that sitewide reductions in deer density have not resulted in equivalent reductions in collision rates (Novak et al. 1999). Thus, the localized management concept was considered an appealing strategy for deer management at SRS.

The population history and management at SRS is different from that of the Adirondacks herd where the only previous test of the localized management concept occurred. The Adirondack population has not been hunted since 1932 and it is characterized by low deer density and an older age structure (Aycrigg and Porter 1997). Female deer in the herd consistently reach older age classes (>10 years, Aycrigg and Porter 1997). In contrast, the SRS population has been subjected to intensive harvest since 1965 that is nonspecific for age and gender. Does typically represent approximately 50% of the harvest. This management has resulted in a young age structure, with less than 4% does harvested in 2002 in the 5.5+ age class. Because the geographic location, population history, age structure, and management were so different from the Adirondacks, we felt that SRS was an appropriate place to examine the assumptions and effectiveness of the localized management concept.

OBJECTIVES AND GUIDE TO THE DISSERTATION

Localized management of white-tailed deer appears to have considerable potential for reduction of deer-vehicle collisions; however, only limited tests of this technique have been conducted to date (Oyer and Porter 2004). The goal of this project is to examine the potential for localized management to be effective in reducing deer-vehicle collisions at the SRS. To address this problem, I have taken 2 separate and complementary approaches. The first specific objective is to examine social and genetic structure in the SRS population to determine the validity of the assumptions underlying the localized management concept. Chapters 2 and 3 are primarily focused on this objective. At the same time, I implemented a series of removal actions meant to simulate a localized management program for deer-vehicle collisions. These management actions were evaluated in terms of observations about genetic and social structure and in terms of effects on population density in the managed areas. These removal actions are the primary subject of chapters 4 and 5.

This dissertation is organized as a series of manuscript-style chapters addressing aspects of the study objectives described above. Chapter 2 examines genetic structure and social interactions of female deer at the level of the kin group identified by Mathews and Porter (1993). Using microsatellite DNA data, I calculated pairwise relatedness and defined probable relationships among 38 deer from a 7,000-ha area of the SRS. Using radiotelemetry or kill location as spatial information, we examined the relationships between spatial and genetic structure to test the hypothesis that kin group structure was consistent with the rose-petal model. The manuscript based on this chapter has been accepted by the *Journal of Wildlife Management* and is currently in press.

Chapter 3 addresses population genetic structure and dispersal in SRS deer at a larger spatial scale. We defined 4 potential subpopulations at the SRS and determined the extent of genetic differentiation among them using microsatellite DNA data. We also determined the extent to which dispersal among SRS deer is biased toward males. The results were considered as they relate to the predictions of the rose petal hypothesis and as they relate to social structure and dispersal observed in white-tailed deer from other locations. This manuscript will be submitted to *Molecular Ecology*.

Chapter 4 and 5 examine the removal actions implemented along 4 major roadways with a history of deer-vehicle collisions at SRS. In chapter 4, I used population genetic analyses to assess the extent to which the deer from removal areas were genetically distinct subpopulations as the localized management concept predicts. I was also able to estimate migration rates from adjacent habitats into the removal areas. Chapter 5 addresses the effects of removal actions on the population density and population distribution of deer in the roadside removal areas. We used 3 population density indices to assess these changes for 2 years following the implementation of removal actions. The manuscripts based on these chapters will be submitted to the *Wildlife Society Bulletin*.

Chapter 6 of the dissertation presents a summary of the findings for all of the manuscript chapters. It also addresses the overall goal of the study to assess the potential of localized management to address deer-vehicle collisions at SRS and provides management recommendations.

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CHAPTER 2

FINE-SCALE GENETIC STRUCTURE AND SOCIAL ORGANIZATION IN FEMALE WHITE-TAILED DEER[1]

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ABSTRACT:

Social behavior of white-tailed deer (*Odocoileus virginianus*) can have important management implications. The formation of matrilineal social groups among female deer has been documented and management strategies have been proposed based on this well-developed social structure. Using radiocollared (n = 17) and hunter or vehicle-killed (n = 21) does, we examined spatial and genetic structure in white-tailed deer on a 7,000-ha portion of the Savannah River Site in the upper Coastal Plain of South Carolina. We used 14 microsatellite DNA loci to calculate pairwise relatedness among individual deer and to assign doe pairs to putative relationship categories. Linear distance and genetic relatedness were weakly correlated (r = -0.08, P = 0.058). Relationship categories differed in mean spatial distance, but only 60% of first degree related doe pairs (full sibling or mother-offspring pairs) and 38% of second degree related doe pairs (half sibling, grandmother-granddaughter pairs) were members of the same social group based on spatial association. Heavy hunting pressure in this population has created a young age structure among does, where the average age is <2.5 years, and <4% of does are >4.5 years old. This, combined with potentially elevated dispersal among young does, could limit the formation of persistent, cohesive social groups. Our results question the universal applicability of recently proposed models of spatial and genetic structuring in white-tailed deer, particularly in areas with differing harvest histories.

Key words: genetics, home range, microsatellites, *Odocoileus virginianus*, radiotelemetry, relatedness, rose-petal hypothesis, Savannah River Site, South Carolina, white-tailed deer.

INTRODUCTION

The white-tailed deer is an economically and ecologically important wildlife species throughout the eastern and midwestern United States. Widespread recovery of deer populations in the eastern United States in the last 50 years has brought about necessary changes in deer management strategies (McShea et al. 1997). The current economic and ecological implications of white-tailed deer and overabundant deer populations are well-established (Conover 1997) and understanding white-tailed deer social organization is important in designing effective management strategies.

Social behavior of white-tailed deer has been extensively studied. Previous studies have shown that female deer form cohesive social groups that use similar habitat ranges for much of the year (Hawkins and Klimstra 1970, Aycrigg and Porter 1997). Dispersal among female deer is typically low (<5%, Kammermeyer and Marchinton 1976, Dusek et al. 1989), although Nelson and Mech (1992) observed 13-20% dispersal in female white-tailed deer in Minnesota and Nixon et al. (1991) observed 40% dispersal in female fawns and 20% dispersal among yearling does in Illinois. In a 30-year series of studies of deer in the Adirondack Mountains in New York, several researchers developed a model for deer population expansion termed the “rose-petal hypothesis” (Porter et al. 1991). This hypothesis proposes that female deer populations expand as a series of overlapping home ranges that are similar to the petals of a rose. According to the model, female offspring are highly philopatric, establish home ranges that overlap that of their mother and have low dispersal rates (Porter et al. 1991). Based on radiotelemetry data, Tierson et al. (1985) identified several social groups of does in the Adirondack Mountains study area that consistently occupied overlapping winter and summer ranges and had low female dispersal (4%). These social groups of associated does formed the basic units of the rose-petal model.

The rose-petal model implies that genetic structure exists in deer populations at the level of relationships among individual deer. Each succeeding generation of females forms approximately concentric rings of home ranges radiating outward. In support of this concept, Mathews and Porter (1993) found that members of a social group were genetically similar according to allozyme analysis and spatially close according to radiotelemetry and visual association data. Therefore, the rose-petal hypothesis predicts a negative correlation between genetic relatedness and spatial distance among female white-tailed deer. Where different social groups have adjacent or overlapping ranges, genetically dissimilar individuals may occur in close spatial proximity. The occurrence of numerous genetically similar doe pairs that are spatially distant suggests that closely related deer do not have overlapping home ranges and are not behaving according to the predictions of the rose petal model. Specifically, does that are either mother-daughter or full siblings (first degree relationship) would have overlapping home ranges (Porter et al. 1991). Furthermore, half-siblings or grandparent-grandchild pairs (second degree) likely would be members of the same social group and would therefore be spatially close. These predictions contrast with those of the "gas diffusion" model of deer behavior, in which deer diffuse or disperse from more populated areas to less populated areas until equilibrium is reached (Porter et al. 1991). In this case, little genetic structure would be apparent in the population and relationships between spatial and genetic distance would be weak or absent.

In application, the rose-petal hypothesis suggests that intensive removal of deer from a small area can create an area of low population density that will persist for more than 10 years (Porter et al 1991). The effort required to manage deer in this limited area is likely less than that needed to reduce population density over a larger area. McNulty et al. (1997) tested this localized management strategy by removing a social group of 14 does from the Adirondack Mountains study area and observing the movements of radiocollared deer ($n = 9$) in adjacent social groups. After the removal, a local reduction in deer density was observed; however, deer in adjacent social groups did not respond by altering their home ranges. More recent analysis of the same removal test indicated that lower deer density persisted for 5 years post-removal (Oyer and Porter 2004). Although deer were present in the removal area, they apparently were descended from either females remaining in the removal area or immigrants from adjacent social groups (Oyer and Porter 2004). Based on these limited tests of its assumptions and effectiveness in a single geographic area, the localized management concept has been widely proposed for managing locally abundant white-tailed deer, especially in urban or suburban settings with deer-human conflicts (e.g., Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004).

The localized management concept has the potential to be an important tool for deer managers in areas where the underlying population model operates. However, testing of the model to date has been limited to the Adirondack Mountains study area. Several characteristics of the Adirondack deer herd are different from those found in other regions of the country, particularly in the southeastern United States. Like many northern deer herds, white-tailed deer in the Adirondacks migrate seasonally between summer and winter ranges (Tierson et al. 1985). The Adirondack study area has not been hunted since 1932, which has resulted in a very old age structure in the herd (Aycrigg and Porter 1997). Despite the lack of hunting pressure, deer densities in the Adirondacks are generally low due to low recruitment and periodic widespread mortality from severe winter weather (Aycrigg and Porter (1997). The influence of these herd characteristics on deer social behavior is not clear, but it could be substantial (Marchinton and Atkeson 1985). Southeastern deer herds are nonmigratory and typically have high recruitment and heavy hunting mortality, which results in a young age structure. To date, studies of deer population structure in the southeast have been at regional scales that do not address the social group structure of the rose-petal hypothesis (e.g., Leberg and Ellsworth 1999, Purdue et al. 2000). For these reasons, an investigation of fine-scale genetic and social structure in a southeastern deer herd is both timely and relevant.

We examined population structure in white-tailed deer in the Coastal Plain of South Carolina to determine whether social organization was consistent with the predictions of the rose-petal hypothesis and to evaluate the potential effectiveness of localized management. We determined the degree of home range overlap and linear distance between point locations for female white-tailed deer. We used microsatellite DNA loci to measure pairwise genetic relatedness among deer. By determining the correlation between genetic and spatial distance measures, we were able to examine socio-spatial structure in the deer herd. Furthermore, we used specific categories of relatedness (e.g., full siblings) to examine their spatial relationship. Together, these analyses allowed us to determine whether social organization was consistent with the predictions of the rose-petal hypothesis.

STUDY AREA

The Savannah River Site (SRS) is an approximately 800-km^2 National Environmental Research Park encompassing portions of Aiken, Barnwell, and Allendale Counties in South Carolina. The SRS is administered by the U.S. Department of Energy (DOE) and managed jointly by DOE and Westinghouse, Inc. While active facilities occupy portions of the site, most of the SRS is undeveloped. The SRS is approximately 68% pine forest and consists primarily of variable-aged stands of longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine (Imm and McLeod in press). Swamps and riparian bottomlands dominated by hardwoods, including oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and blackgum (*Nyssa sylvatica*), occupy 22% of the site. Upland hardwoods, including oaks and hickories (*Carya* spp.), represent approximately 7% of land cover. Forested stands are interspersed with open habitats such as powerline rights-of-way, recent timber harvests, and road/facilities areas. The SRS is within the upper Coastal Plain physiographic province.

The deer herd at SRS has been managed since 1965 by annual dog-drive deer hunts over much of the site. Management sets annual removal goals to maintain a sitewide population of 4,000 animals (5/km^2) to minimize deer-vehicle collisions while maintaining a healthy population. Current population density varies across the site but is generally estimated at 4-6 deer/km^2 in most areas (Novak et al. 1999). Despite the low deer density, deer-vehicle collisions on site roads are considered a management problem. From 1990–2000, the SRS averaged approximately 75 deer-vehicle collisions annually, and data indicate that sitewide reductions in deer density have not resulted in equivalent reductions in collision rates (Novak et al. 1999).

Our study area consisted of approximately 7,000 ha in the upland northwestern portion of the SRS, centered along a major site roadway. Vegetative cover and deer density in the study area were typical for upland portions of the SRS. The area was approximately bisected by Upper Three Runs Creek, which is a major site drainage. Managed hunts were not conducted in the study area during the 2000 and 2001 hunt seasons.

Extensive population and genetic studies of white-tailed deer have been conducted at the SRS using allozyme techniques and hunter-harvested animals. They found that populations in the Savannah River swamp and upland portions of the site differed demographically and genetically (Dapson et al. 1979, Ramsey et al. 1979) and found significant non-random clustering and genetic structure in deer harvested across the site (Scribner et al. 1997). These studies provide evidence for genetic structure in the SRS deer herd at larger landscape scales; however, they did not consider structure at the individual level.

METHODS

Deer Capture

Between January 2001 and August 2002, we captured female white-tailed deer using rocket and drop nets and by darting from vehicles or tree stands. Nets were placed on 0.1–0.2-ha food plots and baited with whole kernel corn and salt. We immobilized deer captured in nets with xylazine hydrochloride administered intramuscularly at 1 mg/kg body weight. We darted deer from vehicles using spotlights and either Cap-Chur (Palmer Cap-Chur Equipment, Inc., Powder Springs, Georgia, USA) or Dan-Inject (Dan-Inject ApS, Borkop, Denmark) dart rifles. Darts were loaded with 3 cc of xylazine hydrochloride (1.8 ml at 100 mg/ml) and Telazol (500 mg in solution). Due to the dense vegetation and large potential escape area, we used Pneu-Dart (Pneu-Dart, Inc., Williamsport, Pennsylvania, USA) transmitter darts to aid in deer recovery. In an effort to sample multiple deer from the same potential social groups, we focused capture efforts in certain locations. However, the dense year-round cover and low deer density limited our ability to identify and target members of apparent social groups.

We aged deer by tooth wear and replacement (Severinghaus 1949). For genetic analysis, we collected approximately 2 cm^2 of ear tissue from the lower edge of one ear with a razor blade. Deer were individually marked with numbered brass ear clips and plastic ear tags and fitted with a 3-year radiocollar with an 8-hour mortality signal (Advanced Telemetry Systems, Isanti, Minnesota, USA). We administered a topical antibiotic on all external wounds and administered the systemic antibiotic tetracycline at 20 mg/kg-body weight by subcutaneous injection. After processing, deer were given an intravenous injection of yohimbine hydrochloride at 0.06 mg/kg body weight to facilitate recovery from the immobilizing drugs. We monitored all deer until recovery before release. All capture and handling work was done in accordance with University of Georgia Institutional Animal Care and Use Committee permit number A2002-10119-0.

Radiotelemetry

We collected year-round radiotelemetry data by triangulation using the loudest-signal method (Mech 1983). We used hand-held receivers and 3-element Yagi antennae to take azimuths from permanently located and geo-referenced triangulation stations. We triangulated deer locations using sequential bearings, taking <20 min to collect the 3-7 azimuths used to estimate the location of an individual deer (Nams and Boutin 1991). We divided days into 4 equal segments of 6 hours each and collected locations approximately equally among the 4 segments. All locations were separated by at least 8 hours to minimize the potential for autocorrelation among locations (Otis and White 1999). The mean angular telemetry error was 8.3° (SE = 0.80) as determined by estimating bearings ($n = 50$) to 10 test transmitters placed at random, geo-referenced locations in the study area. Average transmitter to receiver distance during this study was 470.4 m (SE = 420.2 m).

We used the program LOCATE II to convert telemetry azimuths to UTM coordinates (Nams 1990). We plotted locations in ArcView (ESRI, Redlands, California, USA). For all deer with greater than 30 radiolocations, we estimated home range using the 95% kernel method in the animal movements extension for ArcView. We identified individuals with overlapping home ranges by visual inspection of ArcView polygons. For each pair with overlap, we calculated home range overlap as a percentage of the average total home range for the 2 individuals:

$$O = \frac{A_o}{\left[(A_1 + A_2) \big/ 2 \right]} * 100$$

where O is the percent overlap, A_o is the area of overlap (in m^2), and A_1 and A_2 are the home range areas (in m^2) of deer 1 and deer 2 respectively. This value is equivalent to Cole's index of association (Cole 1949).

In addition to the radiocollared deer, we collected an approximately 20-cm^3 piece of abdominal muscle for genetic analysis from all deer killed during a management hunt in the 7,000-ha study area in September 2002. Hunters were interviewed immediately after the hunt to determine precise kill locations for each deer sampled. Additionally, we obtained muscle tissue samples from all deer killed by vehicle collisions in the study area during the period from April 2001 through December 2002. The locations of all deer-vehicle collisions were recorded using Global Positioning System (GPS).

Genetic Analyses

We froze and stored all tissue samples at -70° C. We extracted DNA from tissue samples using Qiagen DNEasy DNA isolation kits (Qiagen, Inc., Valencia, CA, USA). Following extraction, we quantified DNA concentration in the resulting solution by 1% agarose gel electrophoresis with ethidium bromide staining and used lambda DNA for reference (Sambrook et al. 1989).

Anderson et al. (2002) identified 21 polymorphic microsatellite loci in white-tailed deer from Oklahoma. These loci were evaluated in 13 southern populations of deer and determined to be suitable for use in parentage and other population genetic studies (DeYoung et al. 2003). Based on analyses of 80 randomly chosen individuals from SRS, 14 of these loci were determined to be polymorphic and did not deviate significantly from the expectations of Hardy-

Weinberg equilibrium (HWE) (C. E. Comer, University of Georgia, unpublished data). Following DNA isolation, we used polymerase chain reaction (PCR) to amplify these 14 microsatellite loci using primers and reaction conditions described by Anderson et al. (2002). After amplification, PCR products were loaded onto 12-cm acrylamide microsatellite gels and electrophoresed in an ABI 377 analyzer (Applied Biosystems, Inc., Foster City, CA, USA). To aid in distinguishing loci, primers were fluorescently labeled with 1 of 3 dyes (NED-2 amidite [NED], 6-carboxyfluorescein [6-FAM], or 6-carboxyhexafluorescein [HEX]) as identified in Anderson et al. (2002). An internal size standard (R-500, Genetix, New Milton, U.K.) was also loaded with each sample to allow size identification of microsatellite alleles. Chromatograms derived from microsatellite runs were initially analyzed with GENESCAN (Applied Biosystems, Inc. Foster City, CA, USA), and then imported into GENOTYPER (Applied Biosystems, Inc. Foster City, CA, USA) for characterization of alleles. We evaluated the loci for HWE and linkage disequilibrium (LD) using the web version (3.4) of GENEPOP (Raymond and Rousset 1995). Due to the large number of comparisons, we applied sequential Bonferroni correction to these tests (Rice 1989). We used the program CERVUS to calculate heterozygosity and polymorphic information content (PIC) for all loci (Marshall et al. 1998).

Data Analyses

We examined the relationship between genetic relatedness and spatial distance to examine the extent to which SRS deer behaved in a manner consistent with the rose-petal hypothesis. This hypothesis describes a complex set of behaviors leading to the formation of population structure; therefore, it is difficult to devise a single statistical test to determine its presence or absence. Other authors have noted the difficulty in biological interpretation of population genetics data (Bohonak 1999, Balloux and Lugon-Moulin 2002). Rather than relying on a single test, we used a weight-of-evidence approach to consider evidence in favor of the rose-petal hypothesis. The approach consisted of a series of correlation tests using different subsets of the available data, which was followed by the examination of the spatial characteristics of specific relationship categories.

To assess genetic structure of the population, we performed statistical correlation analyses between genetic distance measures and spatial distance measures. Because it predicts that closely related does form overlapping home ranges, the rose-petal hypothesis predicts a negative correlation between genetic relatedness and spatial separation. That is, we expect more closely related deer pairs to have smaller distances between them. We assessed genetic separation using pairwise relatedness among individual does. We estimated relatedness using the unbiased r_{xy} statistic of Queller and Goodnight (1989). The r_{xy} statistic varies from -1 to 1, with zero indicating the relatedness in a random draw of alleles from the population. A positive value indicates the genotypes of a pair of individuals are more closely related than a random draw from the population. Pairwise relatedness scores were calculated using the program SPAGeDi 1.0 (Hardy and Vekemans 2002). Allele frequencies and background relatedness scores were derived from a larger ($n = 368$) sample of deer from the entire SRS. Using the relatedness scores, we assessed the degree of correlation between relatedness and spatial measures for 3 sets of deer pairs: the set of all does sampled, a subset consisting of only adult deer, and a subset of deer with overlapping home ranges.

For the entire set of deer pairs, we used the linear distance between point locations as the independent spatial variable. Point locations were either kill locations or geometric means of telemetry locations. The SRS management hunts used dogs to drive deer to stationary hunters. However, D’Angelo et al. (2003) showed that deer rarely leave their home range during these hunts. Therefore, kill locations are assumed to occur within normal home ranges for these deer. To assess potential bias from using kill locations versus mean telemetry locations, we conducted a bootstrap simulation analysis using the radiocollared does. For each of 10,000 iterations, the simulation randomly chose (with replacement) a known telemetry location for each deer as a simulated kill location. For each iteration, these simulated kill locations were used to calculate pairwise distances between individuals. We then calculated correlations between the simulated distances and pairwise relatedness. By comparing the correlations with simulated distances to the correlation for these same deer using mean telemetry locations, we were able to assess potential bias due to the use of kill locations in the analysis.

We assessed correlation between linear distance and relatedness using the Mantel test of matrix correspondence (Smouse et al. 1986). The Mantel test compares the correlation between the observed matrices to correlations observed between a large number (n = 10,000) of random permutations of the matrix columns and rows. The test accounts for the fact that the set of all pairwise distances (genetic or spatial) is not independent (Smouse et al. 1986). Mantel tests are a common method for assessment of correlation between genetic and spatial distance matrices (Diniz-Filho and Campos-Telles 2002) and they have been used to compare r_{xy} values and linear distances (e.g., Ohnishi et al. 2000). In addition to the Mantel tests, we assessed genetic structure using the spatial autocorrelation procedure of Peakall et al. (2003). We used the program GenAlEx 5.1 to perform spatial autocorrelation calculations (Smouse and Peakall 1999). For spatial autocorrelation, we set the analysis to consider 12 distance classes of 1 km each and used permutations (n = 999) to derive probabilities associated with the autocorrelation.

Because white-tailed deer fawns typically stay in close association with their mothers for at least 1 year after birth (Hawkins and Klimstra 1970) and dispersal is highest in the fawn and yearling age class, spatial location of fawns may not accurately represent adult range (Nixon et al. 1991, Nelson and Mech 1992). Inclusion of fawns potentially biased our results toward greater correlation between spatial and genetic distance. Therefore, we conducted separate Mantel test and spatial autocorrelation analyses using only adult does that were >1.5 years old at the time of sampling.

For radiocollared does, we assessed the correlation between home range overlap and relatedness. The Mantel test was not applicable in this analysis due to the high number of empty matrix elements (i.e., many doe pairs had zero home range overlap). However, the lack of independence among pairwise values is likely to be less important in this instance because each individual is involved in only a small number of pairwise interactions. Therefore, we calculated Spearman's rank correlation coefficient r_s to assess correlation between home range overlap and relatedness (Ratnayeke et al. 2002). Note that for calculations involving home range overlap, the sign of the correlation coefficient is opposite of that for linear distance (as overlap increases, linear distance decreases).

In a complementary test to the correlation analyses, we examined the spatial relationships of doe pairs related at specified levels. Estimates of relatedness like the r_{xy} score can be used to classify pairs of individuals into relationship categories; however, a likelihood-based approach provides a more powerful method for making these assignments (Blouin 2003). The program Kinship 1.2 allows tests of various hypotheses regarding the relationships between pairs of individuals (Queller and Goodnight 1989). The program calculates a ratio between the likelihood of a given hypothesis (e.g., full siblings) versus a null hypothesis (e.g., unrelated). Based on simulation of many hypothetical pairs (n = 10,000), the program determines the likelihood ratio needed to reject the null hypothesis for a given pair at a user-defined alpha level.

We used Kinship 1.2 to assign all doe pairs to 1 of 3 relationship categories: first degree (including mother-offspring and full sibling pairs), second degree (grandmother-granddaughter, half-sibling, aunt-niece pairs), and unrelated. We then used graphical methods to examine the extent to which these relatedness categories corresponded to differences in spatial distance between pairs. Closer examination of the spatial relationships of doe pairs in each category allowed us to specifically address predictions of the rose-petal hypothesis such as the prediction that closely related deer (e.g., category 1 or 2 related) should share significant portions of their range.

RESULTS

Radiotelemetry

We captured and radiocollared 17 female deer at the SRS in winter/spring 2001 and 2002, including 9 captured in rocket nets and 8 through darting. These included 4 doe fawns (≤1 year old), 4 yearlings (1.0–2.0), 8 adults (2.0–4.5), and 1 older adult (>4.5). Of 17 does, 12 survived through the study period. Two were killed in managed hunts, 1 was killed by a vehicle, and 2 died of unknown causes. One doe made an approximately 8-km dispersal movement in February 2002, when she was approximately 20 months old. A second doe also apparently dispersed. After occupying 1 range for 8 months, she moved approximately 4.5 km in October 2001 when she was 17 months old and stayed in the new range for 2 months. However, she died of unknown causes before sufficient radiolocations were obtained to delineate a new home range. For the correlation analyses, only the natal ranges (pre-dispersal) of these deer were used for spatial calculations. The use of natal ranges for these does provides an upper limit estimate of correlation between genetic and spatial distance compared to adult (post-dispersal) ranges. The remaining 15 does were consistent in their range use and did not show seasonal or dispersal movements.

Home ranges for the 17 does were calculated based on an average of 81 radiolocations (range 43–142). Deer were monitored over an average period of 315 days (range 51–846). Deer were only included if they had >10 radiolocations in at least 2 seasons (winter, spring, summer, fall). Two deer had radiolocations in only 2 seasons, but the remaining 15 were monitored in all 4 seasons. The mean 95% kernel home range size was 197 ha (range 89–365 ha). Of 136 potential radiocollared deer pairs, 17 pairs had home ranges that had an average overlap of 21.1% (range 0.6–77.2%).

We obtained muscle tissue samples from 15 does killed during management hunts within the 7,000-ha study area, from 4 does killed in vehicle collisions, from 1 predated deer, and from 1 capture mortality. With the 17 radiocollared does, the total number of tissue samples was 38 (Fig. 2.1). Overall, we sampled 8 doe fawns, 11 yearlings, 16 adults, and 2 older adults. Based on a deer density of 5 deer/km^2 and a sex ratio near 1:1 (Novak et al. 1999), our sample represents approximately 20–25% of does within the 7,000-ha study area. This percentage is comparable to the 30–35% of does radiocollared in the Adirondacks study leading to the formation of the rose-petal hypothesis (Mathews and Porter 1993). Among the 703 doe pairs, average linear distance between point locations (kill locations or mean of telemetry locations) was 4,690 m (SE 88.2; range 301–11,714).

Microsatellites

Genetic diversity for the 368 deer analyzed is reported in Table 2.1. The mean number of alleles per locus was 11.1 and ranged from 3 to 22. The mean observed heterozygosity for all loci was 0.696 (range 0.375–0.867) and the mean polymorphic information content was 0.681

(range 0.352–0.895). Similar to the results of DeYoung et al. (2003), we did not find evidence for linkage disequilibrium in our samples.

Three microsatellite DNA loci (BM4208, ETH152, and N) deviated from Hardy-Weinberg equilibrium in the entire population of 368 individuals from SRS (Table 2.1). All 3 showed a deficiency of heterozygotes compared to expectations. This may be due to the inclusion of related deer in the larger sample or it may indicate the presence of null alleles in the population at low frequencies (Jarne and Lagoda 1996). The presence of null alleles at high frequency in the population can have implications for relatedness calculations, particularly for parentage analysis (Pemberton et al. 1995). We tested for the presence of null alleles at our loci by comparing the genotypes of several known mother-offspring pairs (n = 9) from SRS. We observed no evidence for null alleles at the 14 loci used in this analysis. We also repeated relatedness and Kinship calculations using only those loci at Hardy-Weinberg equilibrium (n = 11) and found that inclusion of the 3 loci did not alter results or conclusions; therefore, we retained all loci in the analyses. Relatedness calculations revealed a mean r_{xy} of -0.01 for the 703 doe pairs (SE 0.006; range -0.43–0.56), similar to the background mean r_{xy} of -0.016 in the population of 368 deer from SRS.

Correlations

The bootstrap simulation on random kill locations suggested that use of random kill locations tended to underestimate correlation between spatial and genetic distances compared to mean telemetry locations, as 68% of simulated correlations were of lower magnitude than the correlation using telemetry locations. However, the r-value calculated from mean telemetry locations (-0.058) was close to the mean of simulations (-0.048) and within the 95% confidence interval (-0.08 to -0.01) for the simulations. Based on these results, we determined that the magnitude of the impact was relatively minor and that the inclusion of kill locations in the analysis was not likely to result in a true strong correlation being missed.

The Mantel test results revealed a weak correlation between linear distance and relatedness (correlation = -0.08, $P = 0.058$) for the set of all does sampled. As further confirmation that this result was not due to the inclusion of kill locations in the spatial distance matrix, we conducted a second Mantel test using only the 17 radiocollared does (136 doe pairs) for which we had mean telemetry locations. With this subset, the correlation was even weaker (-0.06, $P = 0.24$). The results of spatial autocorrelation analyses were similar to the Mantel tests. We observed a weak correlation ($r = 0.036$, $P = 0.003$) at the smallest distance class and no autocorrelation at greater distance classes. The shape of the correlogram most closely resembled that typical for a general absence of spatial pattern as defined by Diniz-Filho and Campos-Telles (2002). Restricting the analysis to adult does eliminated 8 doe fawns from the Mantel test. The Mantel test correlation for adult does ($n = 30$) also indicated a weak correlation between linear distance and relatedness (correlation = -0.071, $P = 0.14$). The spatial autocorrelation analysis for adult deer only produced similar results with marginally significant autocorrelation at the smallest distance class ($r = 0.038$, $P = 0.021$).

Correlation analysis for the subset of doe pairs with overlapping home ranges showed a stronger correlation between home range overlap and relatedness for these deer ($r_s = 0.55$, $P = 0.02$). To test whether the use of home range overlap versus linear distance accounted for the difference in results, we also calculated Spearman's correlation for the same subset of deer pairs using the linear distance measure. The results were not substantially different except for the sign ($r_s = -0.51$, $P = 0.04$), which was expected (see methods).

Relationship Categories

Assigning the 703 doe pairs to relationship categories resulted in 10 pairs with first degree relatedness, 29 with second-degree relatedness, and 664 unrelated (Table 2.2). Simulations in the Kinship program showed that distinguishing second-degree related pairs from unrelated pairs in our data was difficult, explaining the relatively high Type II error rate for this category. The type II error rate in this analysis is the probability of falsely rejecting the null hypothesis and incorrectly assigning second-degree related pairs to the unrelated category. However, we chose to minimize the chance that unrelated pairs were incorrectly assigned to higher relationship categories (indicated by *P* = Type I error rate). Box plots showed a slight upward trend in median distance between pairs from more closely related pairs to less related pairs (Fig. 2.2). However, we observed a high degree of overlap in distances among the 3 categories.

DISCUSSION

We found that the strength of association between genetic relatedness and spatial separation in female white-tailed deer varied depending on the set of deer considered in the analysis. Among does with overlapping home ranges (spatially close), increased relatedness was associated with a greater degree of home range overlap and smaller linear distance. In general, these results are consistent with the predictions of the rose-petal hypothesis. However, when all available doe pairs were included in the analysis the relationship was considerably weaker, suggesting that female deer were not forming social groups that follow a rose-petal pattern.

Of the 17 radiocollared doe pairs with overlapping home ranges, 9 had negative r_{xy} scores indicating they were less related than a randomly drawn pair of individuals from the population. Five of these 9 pairs had only minor (<10%) degrees of home range overlap, but the remaining 4 pairs had between 13% and 27% home range overlap. While these data did not support the rose petal hypothesis, some overlap of home ranges between unrelated deer at the boundaries of social groups is consistent with the model. Among the 136 doe-pairs in which both members were radiocollared, 8 pairs were classified as first or second-degree related pairs. Of these 8 pairs, 5 (63%) showed no overlap in their 95% kernel home ranges. The remaining 3 pairs showed a high degree of overlap (mean = 49%, range 22–77%). One radiocollared doe pair was in the first-degree relationship category; they shared 77% overlap in home range. These 2 deer were captured together when 1 was a fawn and the other was 4.5 years old. Genetic data confirmed this was a mother-daughter pair.

Using the spatial distance between doe pairs, we determined that many closely related doe pairs in the SRS herd were not associated spatially. In their study of social organization in the Adirondacks, Mathews and Porter (1993) delineated 8 social groups consisting of 3-9 does each. The maximum cumulative home-range size for a social group based on 95% minimum convex polygons was 7.2 km^2 (range 1.6–7.2 km^2; Mathews and Porter 1993). Mean home range sizes in the Mathews and Porter (1993) study were similar to or slightly larger than those observed at SRS (240 ha vs. 197 ha); therefore, this provides a conservative estimate of expected social group size. A social group range size of 7.2 km^2 corresponds to a circle with a diameter of approximately 3,000 m. As a conservative estimate, the distance between any 2 points within the home ranges of deer in the same social group should be less than 3,000 m. Among the 29 doe pairs with second-degree relatedness, the linear distance between point locations was greater than 3,000 m for 18 (62%) indicating that only 38% were probable members of the same social group. The mean distance between point locations was almost 4,000 m, and the maximum distance was over 10,000 m. In the 10 doe pairs with first-degree relatedness, 4 pairs (40%) were more distant than 3,000 m, including 1 pair that was over 8,800 m apart. These results indicate that at SRS only 38% of does that are second degree related (grandmother-granddaughter, half-sibling, and aunt-niece) and 60% of does that are first-degree related (mother-daughter or full sib) remain socially affiliated and maintain overlapping home ranges. Eliminating doe pairs that include at least 1 fawn indicates that related adult deer are even less likely to be members of the same social group. Among adult does, 40% of first-degree related doe pairs and 27% of second-degree related doe pairs had a spatial separation consistent with membership in the same social group.

Overall, our results indicated a low degree of genetic structuring at the individual level among female deer at the SRS. These results are in contrast with previous studies showing a high degree of genetic structuring in female deer in this region (Purdue et al. 2000). However, Purdue et al. (2000) based their conclusions primarily on differences in mitochondrial DNA haplotypes. They found considerably less structure in biparentally-inherited allozyme data. Furthermore, that study considered a much larger spatial scale than this study. Sample locations in Purdue et al. (2000) were >25 km apart, and the entire SRS (>800 km^2) is considered a single sample location. The maximum dispersal distance of 50 km described in Purdue et al. (2000) encompasses the entire 7,000-ha study area considered here. While their study provides an enlightening analysis of spatial and genetic structure in the southeast region, it does not address genetic structure at the level of the individual and the social group. Therefore, the results of Purdue et al. (2000) are fundamentally different in scale, and our results do not directly contradict theirs.

In their analysis of social and genetic structure among white-tailed deer in the Adirondacks, Mathews and Porter (1993) identified social groups based on spatial characteristics and then used allozyme data to determine whether these groups were genetically distinct. In an alternative approach, we used more precise microsatellite data to identify genetically similar individuals and to examine the spatial relationships among these individuals. The patterns we observed in spatial and genetic distances were not consistent with the persistent, tightly bound social group structure described for the rose-petal hypothesis (Porter et al. 1991). A possible explanation for the weak correlation between spatial and genetic distances is that matrilineal social groups at SRS were not geographically independent as described by Mathews and Porter (1993). That is, social groups were present, but several such groups shared common spatial range. This also accounts for our observation that several pairs of does with significant home range overlap were apparently unrelated. However, this scenario would be more likely if population density were elevated compared to the Adirondack range. Population density at SRS is low and generally comparable to that in the Adirondacks during the period of Mathews and Porter (1993). More importantly, this explanation does not account for our observation of numerous closely-related deer pairs that are spatially distant. Although we were unable to reject this hypothesis completely, it was not adequate to explain all of our observations.

The alternative explanation is that differences between our study area and the Adirondack study area prevented the formation of a rose-petal type social structure among SRS does. Important characteristics of the deer herd that could affect the social cohesiveness include such interrelated factors as migratory behavior, age structure, harvest history, and dispersal characteristics. The Adirondack deer herd is migratory, and deer make predictable seasonal movements between summer and winter ranges (Tierson et al. 1985). Seasonal group movements to and from winter range may strengthen social bonds and group cohesiveness (Nelson 1998). Like most southeastern deer herds, the SRS deer showed no consistent seasonal range changes.

The most striking difference between the Adirondack and SRS deer herds is the harvest history. The Adirondack herd has not been hunted since 1932 and female deer consistently reach older age classes (>10 years; Aycrigg and Porter 1997). At the SRS, annual harvest is extensive: in 2002, hunters took 1,318 deer out of an estimated sitewide population of 5,500 (24%). Does generally represent approximately 50% of harvested deer (52% in 2002; 50% in 2001). This high harvest rate among female deer has resulted in a young age structure among SRS does (Novak et al. 1999). In the 2002 harvest, 71% of does killed were <3 years old. Less than 4% of harvested does were in the 5.5+ age class. Age structure among female deer may be an important factor in the establishment of social structure. Aycrigg and Porter (1997) found that matriarchal females were usually does >5 years of age and that deer in this age class showed the greatest degree of spatial structure. They found little spatial pattern in the home ranges of does <5 years of age.

A higher dispersal rate among female white-tailed deer at SRS could contribute to a pattern consistent with that observed in this study, where the subset of deer with overlapping home ranges showed more genetic and spatial structure. Dispersers are deer that make long distance movements and establish home ranges separate from their natal range (Nelson and Mech 1992). At larger spatial scales, including all deer pairs, the analysis included both “disperser” does and “resident” does (non-dispersers). Dispersing deer were not related to other does close to their new home range, so their inclusion tended to weaken the association between spatial and genetic distances. However, limiting the analysis to those deer with overlapping home ranges reduced the proportion of pairs including a disperser and eliminated pairs of highly related individuals with high distances between them (i.e., a disperser and its mother or sibling). Therefore, the association between spatial and genetic distances would be expected to be stronger with this subset of deer.

Two lines of evidence suggest that dispersal rates among SRS does may be elevated relative to those observed in the Adirondacks where the rose-petal hypothesis was formed. First, we observed 2 putative dispersals (12%) among the 17 radiocollared does in this study. However, dispersal in white-tailed deer typically occurs in the fawn or yearling age class (Hawkins and Klimstra 1970, Nelson and Mech 1992). Eight radiocollared deer were in the yearling or fawn age class when captured, including both deer that made putative dispersal movements. These data indicate a potentially higher (25%) dispersal rate among young does at SRS. Our radiotelemetry study was not designed specifically to address dispersal, and the small number of doe fawns collared limits the direct evidence for elevated dispersal. However, the genetic analyses provide additional evidence for elevated dispersal rates. The only plausible explanation for closely-related deer pairs that are spatially very distant is that 1 or both members of the pair dispersed from their natal range in the past. With >60% of second-degree related pairs and 40% of first-degree related pairs separated by distances inconsistent with social group membership, our analyses suggest that dispersal has been a common occurrence.

High mortality among mature does has been associated with greater dispersal of female fawns. Nelson and Mech (1981) found that orphaned doe fawns in Minnesota showed erratic wandering movements that might indicate dispersal. Etter et al. (1995) found orphaned female fawns dispersed almost twice as often as non-orphaned fawns in Illinois. Annual mortality among does at SRS is approximately 25%. Novak et al. (1991) found that SRS hunters tended to target older age classes preferentially, so mortality among mature does may be even higher. The resulting high orphaning rate could contribute to elevated dispersal rates among female deer.

While our data do not provide definitive evidence for high dispersal rates among SRS does, elevated rates of dispersal provide a logical explanation for our observations.

MANAGEMENT IMPLICATIONS

Our results examine the applicability of the rose-petal model that underlies the localized management concept. The implications for localized management are currently unclear. The literature includes examples where localized management is recommended based on data showing high annual range fidelity (Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004). Our data indicate that such widespread recommendations should be made with caution. Female deer at SRS >2 years old exhibited high range fidelity, but little genetic structure was present in the herd. Using a population modeling approach to examine deer in a suburban environment, Porter et al. (2004) found that the ability to achieve a stable population size through culling or contraception was sensitive to the rate at which does dispersed into the removal area. Culling rates in excess of 75% were necessary to achieve a stable population when dispersal was 25% (Porter et al. 2004). Elevated dispersal rates among young does could render the localized management concept less useful if vacant habitats are quickly recolonized by dispersing females. With increasingly liberal antlerless harvests in most states, female age structure in many herds may be more similar to that observed at SRS than to the older age structure present in the Adirondack deer herd. This underscores the need to develop a more complete understanding of social, genetic, and spatial structure in a deer herd prior to implementing management programs that rely on white-tailed deer social behavior.

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Table 2.1. Locus name, number of alleles, observed heterozygosity, expected heterozygosity, *P*-value for Hardy-Weinberg equilibrium (HWE), and polymorphic information content (PIC) for 14 microsatellite DNA loci genotyped for 368 white-tailed deer from the Savannah River Site, Aiken, South Carolina, 2001-2002.

		Heterozygosity			
Locus[a]	Alleles	Observed	Expected	HWE *P*-value[b]	PIC
BL25	6	0.623	0.671	0.205	0.624
BM4208	20	0.861	0.903	< 0.001[b]	0.895
BM6506	13	0.820	0.823	0.007	0.803
BovPRL	3	0.513	0.523	0.926	0.409
Cervid1	14	0.836	0.831	0.304	0.810
D	10	0.824	0.838	0.561	0.819
ETH152	12	0.750	0.822	< 0.001[b]	0.799
INRA011	6	0.594	0.610	0.333	0.571
K	7	0.484	0.464	0.192	0.409
N	22	0.789	0.885	0.001[b]	0.874
O	6	0.375	0.428	0.021	0.352
OarFCB193	13	0.616	0.579	0.069	0.561
P	8	0.791	0.768	0.192	0.732
Q	16	0.867	0.881	0.497	0.870

[a] Locus names from Anderson et al. (2002).

[b] Indicates locus not in Hardy-Weinberg equilibrium after Bonferroni correction.

Table 2.2. Number of pairs (*n*), type I and type II error rates, mean distance between point locations (m), and mean relatedness scores (r_{xy}) for white-tailed deer does in 3 relatedness categories at the Savannah River Site, Aiken, South Carolina, 2001-2002.

		Error Rate			
Relationship[a]	*n*	Type I	Type II	Distance	r_{xy}
1st Degree	10	0.01	0.036	3,303	0.397
2nd Degree	29	0.05	0.304	3,872	0.196
3rd + Degree	664			4,746	-0.026

[a] Membership in relationship categories was determined from genetic data using the program Kinship 1.2.

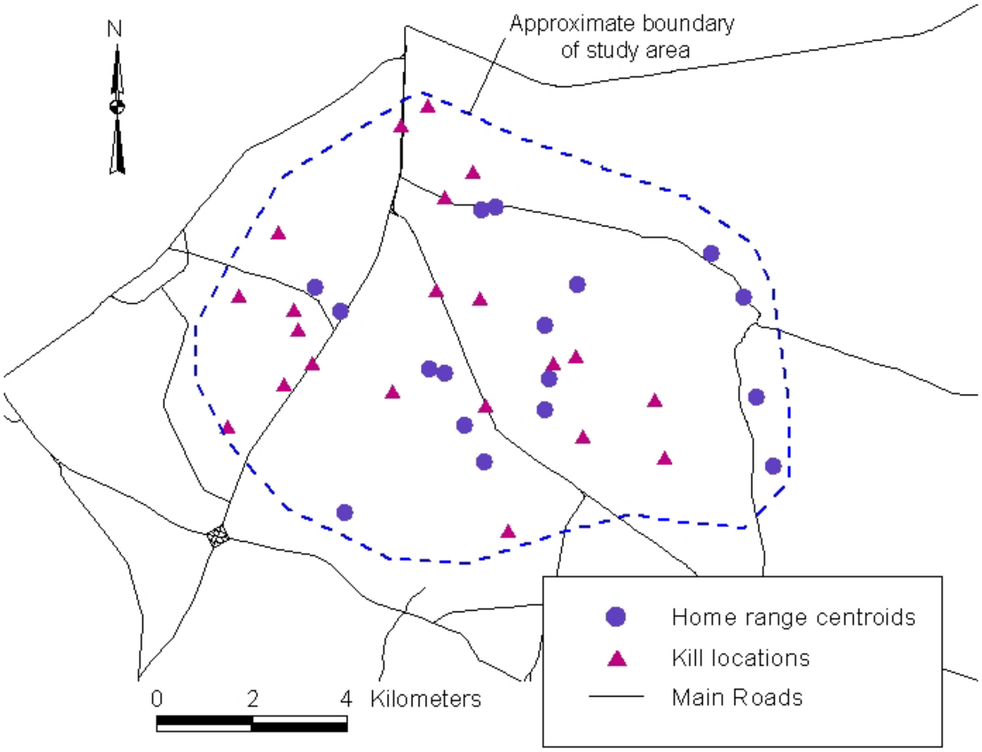

Fig. 2.1. Home range centroids (for radiocollared deer) and kill locations for 38 female white-tailed deer used in population structure analyses at the Savannah River Site, Aiken, South Carolina, 2001–2002. The dashed line shows the approximate boundary of the study area for this study.

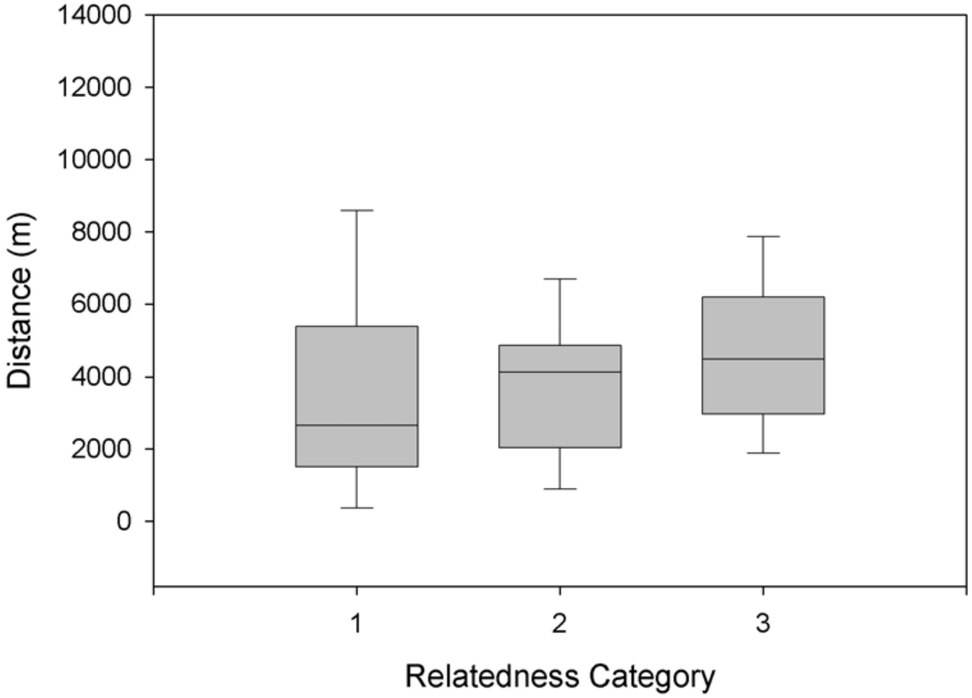

Fig. 2.2. Linear distances (meters) between white-tailed does for all doe pairs in 3 relatedness categories at the Savannah River Site, Aiken, SC, 2001–2002. Boxes show median distance and 25th and 75th percentiles. Whisker bars show 10th and 90th percentiles.

CHAPTER 3

GENETIC SUBSTRUCTURE AND DISPERSAL IN A HEAVILY HARVESTED WHITE-TAILED DEER POPULATION[2]

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[2] Comer, C.E., T.C. Glenn, G.J. D'Angelo, J.C. Kilgo, and K.V. Miller. To be submitted to *Molecular Ecology*.

ABSTRACT

Despite previous investigations, the sociobiology of white-tailed deer (*Odocoileus viginianus*) across their range remains poorly understood. Evidence of genetic structure and male-biased dispersal has been documented in some habitats and geographic areas. However, this species exhibits great plasticity in social behavior in response to a variety of habitat and geographic factors. We evaluated population genetic structure and dispersal at the landscape scale using 14 microsatellite DNA loci in deer from an intensively managed population at the Savannah River Site in the upper Coastal Plain of South Carolina. Analysis of population structure using F_{ST} analysis and Bayesian clustering techniques revealed little differentiation among subpopulations. Sex biases in dispersal were not significant based on corrected assignment indices and sex-specific F_{ST}. These results contrast with evidence for genetic structure and sex-biased dispersal in less intensively managed populations and emphasize the behavioral plasticity characteristic of this species. Putative breeding excursions by females may be an important mechanism of gene flow. A lack of well-developed social structure due to the high harvest level provides a logical explanation for our results.

INTRODUCTION

Many species exhibit spatial genetic structuring because of limitations in gene flow among populations. Gene flow tends to homogenize populations, but geographic barriers to migration or isolation by distance can prevent gene flow and result in local adaptation, differentiation, and eventually speciation (Slatkin 1987). Understanding gene flow and population structure is important in basic population ecology and it has implications for conservation biology and wildlife population management (Balloux and Lugon-Moulin 2002). Genetically isolated populations show reduced heterozygosity and allelic richness, with potentially negative effects on fitness and long-term viability (Nei et al. 1975; Luikart and Cornuet 1998). Reliable delineation of the spatial extent of populations is important in the design of appropriate conservation plans for declining species. Management strategies based on assumptions about population structure also have been proposed for abundant species (Porter et al. 1991).

Dispersal is the primary mechanism by which genetic material is mixed among spatially separate populations. Specifically, natal dispersal is the permanent movement of an individual from its point of origin to a different location where it breeds (Greenwood 1980). Many vertebrate species show significant sex-biases in dispersal rates, with male-biased dispersal most common among mammals and female-biased dispersal most common among birds (Greenwood 1980). A variety of hypotheses have been proposed to explain the evolution of sex-biased dispersal, including mate competition, resource competition, inbreeding avoidance, and primary mating system (Dobson 1982, Pusey 1987, Perrin and Mazalov 2000). In addition to the evolutionary significance of sex-related differences in dispersal rates, they can influence the formation of genetic population structure and they can provide insight into the social structure and kin interactions of wildlife populations.

Highly variable microsatellite DNA loci can provide important information about population structure and gene flow (Balloux and Lugon-Moulin 2002, Goudet et al. 2002). Most traditional methods of analyzing population differentiation have used approaches based on either Wright's (1978) F_{ST} or Slatkin's (1995) R_{ST}. More recently, assignment-based approaches also have been used (Paetkau et al. 1995). These approaches require *a priori* definitions of subpopulation boundaries. However, recently developed Bayesian clustering techniques do not require predefined subpopulations and can test multiple hypotheses regarding the number of subpopulations (Pritchard et al. 2000). These techniques are particularly useful where no obvious geographic barrier separates populations.

Dispersal in wild populations can be estimated directly by radiotelemetry or mark-recapture techniques or indirectly by genetic methods (Slatkin 1987, Wilson et al. 2004). To examine sex-biases in dispersal, genetic methods have often included comparing biparentally inherited nuclear DNA markers with maternally inherited mitochondrial DNA markers. However, differences in mutation rate or effective population size make direct comparisons of the different types of markers difficult. New analytical techniques based on sex-specific F_{ST} values and assignment tests have been used effectively to detect sex-biased dispersal using only biparentally inherited microsatellite markers (Mossman and Waser 1999, Goudet et al. 2002).

White-tailed deer provide an interesting study of population structure and dispersal due to their economic and ecological importance in North America and the variability in social structure that has been observed for this species (Marchinton and Atkeson 1985). Most field studies of social behavior in white-tailed deer have shown a highly developed social structure among females based on highly persistent matriarchal kin groups (Hawkins and Klimstra 1970, Aycrigg and Porter 1997). Field studies of dispersal generally have shown a bias towards greater dispersal of males and greater philopatry among females (Kammermeyer and Marchinton 1976, Nelson and Mech 1984). Population genetic studies have shown differentiation of white-tailed deer populations at the state or regional level using mitochondrial DNA and microsatellites (Ellsworth et al. 1994, DeYoung et al. 2003a) and at the landscape scale with allozyme data (Mathews and Porter 1993, Scribner et al. 1997). Based on a comparison of maternally inherited mitochondrial DNA and biparentally inherited allozymes, Purdue et al. (2000) concluded that males dispersed more than females in the Southeast and that females rarely dispersed greater than 50 km. However, differences in management history and habitat can produce profound changes in social behavior and dispersal in white-tailed deer. Using radiotelemetry and microsatellite data, Comer et al. (2005) found that female deer from a heavily harvested herd in South Carolina did not show persistent kin group structure. In an area of Illinois that was highly fragmented by agriculture and subject to heavy hunting pressure, Nixon et al. (1991) observed approximately equal rates of dispersal among male and female deer. In this study, we looked at population genetic structure and dispersal at the landscape scale in an intensively managed population.

We conducted this study at the Savannah River Site (SRS), an approximately 800-km^2 National Environmental Research Park encompassing portions of Aiken, Barnwell, and Allendale Counties, South Carolina. The deer herd at SRS has been managed since 1965 by annual dog-drive deer hunts over much of the site. Deer hunts are nonselective for age and sex and have been highly successful in maintaining low population density across the site (Johns and Kilgo in press). The harvest management has resulted in an approximately even sex ratio and a young age structure (Novak et al. 1999). Previous work at the SRS used allozyme analysis to suggest that populations in the Savannah River swamp and upland portions of the site differed genetically (Ramsey et al. 1979). In a separate allozyme study, Scribner et al. (1997) found significant non-random clustering at individual loci in deer harvested across the site; however, the location and size of clusters varied among years. Our study used more variable multilocus microsatellite data to examine population genetic structure and dispersal. Previous work has suggested that social and genetic structure at SRS differed from that observed in other populations with different harvest histories (Comer et al. 2005). The objectives of this study were to examine population genetic structure and sex-biased dispersal at the landscape scale and to estimate the potential influence of harvest history on these parameters.

MATERIALS AND METHODS

Sampling and DNA Extraction

We collected tissue samples from deer at the SRS between 17 November 2001 and 11 December 2002. The majority of samples were abdominal muscle tissue collected from deer harvested during management hunts; however, a small percentage of samples were ear tissue collected from captured deer as part of a radiotelemetry study (Comer et al. 2005). We also opportunistically collected muscle tissue samples from deer hit by vehicles and from other mortalities. All individuals were sampled from 1 of 4 subpopulations roughly centered on major site roadways (Fig. 3.1). These subpopulations occupy spatial areas of approximately 61 km^2.

We froze all tissue samples within 8 hours of collection and stored them at -70° C until extraction. We extracted DNA from tissue samples using Qiagen DNEasy DNA isolation kits (Qiagen, Inc., Valencia, CA, USA), following the recommended protocol except that we incubated samples overnight with proteinase K and we used 2 elutions of 100 µl each to remove DNA from the column. Following extraction, we quantified DNA concentration in the resulting solution by 1% agarose gel electrophoresis with ethidium bromide staining and used lambda DNA for reference (Sambrook et al. 1989).

Microsatellite Analysis

We used polymerase chain reaction (PCR) to amplify 14 of the 21 microsatellite loci (BL25, BM4208, BM6506, BovPRL, Cervid1, D, ETH152, INRA011, K, N, O, OarFCB193, P, Q) identified by Anderson et al. (2002) for white-tailed deer. We conducted initial screening on the remaining 7 loci (BM203, BM415, BM848, BM6438, ILSTS011, OCAM, R) but discarded them due to problems with amplification, consistent departures from Hardy-Weinberg equilibrium (HWE) on an initial set of samples, or improper segregation of alleles based on known mother-offspring pairs (*n* = 9). We followed the PCR protocols outlined by Anderson et al. (2002) and labeled one primer of each primer pair with fluorescent dye as described therein. After amplification, PCR products were loaded onto 12-cm acrylamide microsatellite gels and electrophoresed in an ABI 377 analyzer (Applied Biosystems, Inc., Foster City, CA, USA). An internal size standard (R-500, Genetix, New Milton, U.K.) was also loaded with each sample to allow size identification of microsatellite alleles. Chromatograms derived from microsatellite runs were initially analyzed with GENESCAN (Applied Biosystems, Inc. Foster City, CA, USA), and then imported into GENOTYPER (Applied Biosystems, Inc. Foster City, CA, USA) for characterization of alleles. We evaluated the loci for HWE in each population using the web version (3.4) of GENEPOP (Raymond and Rousset 1995a). Due to the large number of comparisons, we applied sequential Bonferroni correction to these tests (Rice 1989). Previous evaluations of these loci have shown no evidence of linkage between loci (Anderson et al. 2002, DeYoung et al. 2003b) except for one instance showing linkage between the BM848 locus and 2 others (DeYoung et al. 2003a). However, we excluded the BM848 locus from our analysis for other reasons. Comer et al. (2005) found that these 14 loci were unlinked in the SRS population.

Subpopulation Differentiation Analysis

We assessed genetic differentiation in the population using several methods. Based on the 4 subpopulations defined by proximity to major site roadways, we conducted F_{ST} and R_{ST} analysis using the program ARLEQUIN (Schneider et al. 2000). The ARLEQUIN program uses an analysis of molecular variance (AMOVA) framework to allocate total variance to either among-populations or within-populations components (Excoffier et al. 1992). We used 10,000 permutations to assess the significance of the AMOVA results. We also used exact tests of population differentiation to calculate pairwise differentiation for all subpopulation pairs based on both F_{ST} and R_{ST} values. This test uses a Markov chain Monte Carlo (MCMC) simulation (100,000 steps, 4,000 step dememorization) to test the hypothesis of a random distribution of individuals between populations (Raymond and Rousset 1995b).

Our designation of subpopulations was not based on geographic barriers between the subpopulations; therefore, it is possible that we did not capture existing genetic subdivisions in the population. The Bayesian clustering algorithm in the program STRUCTURE allows the user to test several values for the number of subpopulations (K) to determine the most likely configuration (Pritchard et al. 2000). Individuals are assigned to subpopulations probabilistically and MCMC analysis is used to infer the probability of each value of K. We ran 5 independent runs for each value of K from 1 to 8 using 1,000,000 MCMC steps and a burnin period of 50,000. We assumed admixture between subpopulations and correlated allele frequencies (Falush et al. 2003). The STRUCTURE program allows the user to compare the posterior probabilities of the various values of K and choose the optimal K based on the log-likelihood of K.

Sex-biased dispersal analysis

We used FSTAT 293 to calculate 3 tests for sex-biased dispersal: sex-specific F_{ST}, mean assignment index (AI), and variance of AI (Goudet 2001). Tests for sex-biased dispersal require exclusion of predispersal individuals (Goudet et al. 2002). The majority of dispersal in white-tailed deer occurs between 0.5 and 1.5 years of age; therefore, we excluded deer <1.5 years old from these calculations. The FSTAT program used a randomization approach with 10,000 iterations to assess the one-tailed significance of sex-biased dispersal tests. Thus, our tests addressed the null hypothesis that male deer do not disperse at a greater rate than female deer.

Among the several tests for sex-biased dispersal available in FSTAT, Goudet et al. (2002) found that the F_{ST} test was the most powerful, followed by the two AI-based tests. The population F_{ST} value expresses the proportion of genetic variance that exists among subpopulations. If one sex disperses more than the other, we expect that populations will be less differentiated for that sex. Therefore, F_{ST} should be lower for the dispersing sex. The FSTAT program uses Weir and Cockerham's (1984) unbiased estimator of F_{ST}. The AI approach uses allele frequencies to calculate the probability of each genotype occurring in its population of origin (Paetkau et al. 1995). The FSTAT program follows the approach of Favre et al. (1997) to derive corrected AI (AI_c) values that are modified to account for population average AI. The mean and variance of AI_c values for males and females are then compared. The genotypes of immigrant individuals are less likely to occur in the subpopulation where they were sampled; therefore, they have lower AI_c values. The dispersing sex in any subpopulation consists of a mixture of resident and immigrant individuals; therefore, we expect a lower mean AI_c and higher variance of AI_c for that sex.

RESULTS

Sampling and Microsatellite Analysis

We obtained samples from 384 deer at the SRS, including 192 males and 192 females (Table 3.1). Of these, 77 were juveniles, leaving 307 adult individuals for the sex-biased dispersal analysis. Measures of genetic diversity parameters were similar across the 4 subpopulations sampled (Table 3.2). All populations showed a slight deficiency in mean observed heterozygosity compared to expectations; however, only one locus (ETH152) deviated significantly from HWE in any subpopulation after Bonferroni correction (Table 3.2). We tested for the presence of null alleles at this locus by comparing several ($n = 9$) fetal genotypes to known mothers. No evidence of null alleles was detected in the genotype comparisons. The deviation from HWE was most likely the result of the incidental inclusion of related individuals in the sampled populations. Because of this and because the locus deviated from HWE in only 1 of 4 subpopulations, we retained the ETH152 locus in our analyses.

Subpopulation differentiation

The results of both F_{ST} and R_{ST} analyses suggested that the 4 subpopulations were not genetically differentiated. We report only the F_{ST}-based results here because the results of the two analyses were qualitatively similar and F_{ST} analyses generally perform better for weakly structured populations (Balloux and Goudet 2002; Balloux and Lougon-Moulin 2002). Pairwise F_{ST} values ranged from 0.0041 to 0.0121 (Table 3.3). The AMOVA results support these data, as 99.4% of genetic variation was within subpopulations (SS = 3,819, 767 d.f.). The exact test for population differentiation found no differences between subpopulations based on F_{ST} (Table 3.3).

The results of the STRUCTURE analysis confirmed that little genetic structure was present in the SRS population. The highest log-likelihood occurred at K = 1, or a single genetically panmictic population. The mean logP(k/x) for 5 runs with K = 1 was -17,974. The values of logP(k/x) for K = 2, 3, and 4 were -18,348, -18,625, and -18,812 respectively. For all values of K > 4, the log likelihoods were <-19,412. These numbers corresponded to a probability approaching 1.0 that the true value of K is 1. Additionally, the proportions of individuals assigned to subpopulations at all K > 1 were symmetric, again suggesting that no substructure existed (Pritchard et al. 2000).

Sex-biased dispersal

The results of all three tests for sex-biased dispersal suggested a male bias in dispersal; that is, males had a lower F_{ST}, lower mean AI_c, and higher variance of AI_c (Table 3.4). However, the results for F_{ST} and mean AI_c were not statistically different at $\alpha = 0.05$. The results for AI_c variance were marginally different; however, this difference was not significant after Bonferroni correction.

DISCUSSION

Population Structure

Our analyses demonstrate that the SRS deer population functions as a single, panmictic unit at the scale of this study. This contrasts with the results of previous studies of genetic structure among deer at SRS; however, methodological and temporal differences between the studies make direct comparison difficult. Previous work suggested that nonrandom genetic clusters existed in the population at a single allozyme locus (Scribner et al. 1997) and that the swamp and upland populations were genetically distinct (Ramsey et al. 1979). The data for these studies were collected 25 years before this study at a time when SRS deer management included both still and dog hunting. Multilocus analyses found no significant differences between subpopulations at SRS (Smith et al. 1990).

The lack of population structure also contrasts with numerous studies showing genetic structure or subdivision at state or regional scales (Kennedy et al. 1987, Ellsworth et al. 1994a, Ellsworth et al. 1994b, Leberg et al. 1994, Purdue et al. 2000, DeYoung et al. 2003). These studies were conducted over a considerably larger spatial scale, raising the possibility that genetic structure among white-tailed deer emerges only at larger scales. Indeed, the SRS was considered a single population for sampling purposes in several of these studies (Ellsworth et al.

1994a, 1994b, Purdue et al. 2000). Purdue et al. (2000) found that female deer in the Southeast (including samples from SRS) had a maximum functional dispersal distance of 50 km based on the distribution of mitochondrial haplotypes. Distances between our subpopulations were considerably less than 50 km, possibly explaining the lack of differentiation we observed. It is worth noting that Purdue et al. (2000) found considerably less structure using biparentally inherited allozyme markers. However, Mathews and Porter (1993) found genetic differentiation in allozyme markers at the local scale (smaller than our study) in New York. Therefore, while genetic structure appears to be more common at large scales, subpopulation differentiation at smaller scales can be observed in some circumstances.

Differences in population history and social structure can account for the observed lack of subpopulation differentiation at the SRS. In many parts of the Southeast, restocking of deer contributed to rapid repopulation following historic population declines. Genetic effects from these restockings are still evident in differentiation of populations in Mississippi and across the Southeast (Kennedy et al. 1987, DeYoung et al. 2003). South Carolina is unusual in the Southeast in that no deer were imported from outside the state as part of stocking efforts. All deer currently on the SRS are believed to be descended from remnant individuals surviving in the Savannah River swamp when the site was acquired in 1951 (Johns and Kilgo in press). This single population of origin may contribute to the current lack of genetic structure at SRS and to differences between our results and those of previous studies.

Current management practices for the SRS deer population may provide the most important explanation for the lack of subpopulation differentiation. Social factors, particularly persistent matriarchal structure and female philopatry, have been used frequently to explain local scale and larger scale genetic structure in white-tailed deer (Mathews and Porter 1993, Purdue et al. 2000, DeYoung et al. 2003). A model for deer population expansion based on this phenomenon was formulated and termed the "rose-petal hypothesis" (Porter et al. 1991). The formation and persistence of this social structure is reliant on the presence of older (> 4.5 years), matriarchal does around which the structure forms (Aycrigg and Porter 1997). Traditional deer management, with a heavily male-biased harvest, allows female deer to survive to older age classes and may promote the formation of matriarchal groups. In contrast, the harvest at SRS is both intensive and unbiased with regard to sex, leading to nearly equal sex ratios and a young age structure among does (Novak et al. 1999). Comer et al. (2005) found that social structure was weakly formed or nonexistent among does at SRS and attributed these observations to harvest management. The absence of these social factors may explain the lack of subpopulation differentiation and the panmictic population we observed at SRS.

Sex-biased dispersal

Our results suggest that dispersal in the SRS population is biased towards males, but that the difference was not sufficiently great to be consistently detected by indirect genetic methods. Previous studies have used radiotelemetry or mark-recapture techniques to directly measure dispersal rates among males and females (Kammermeyer and Marchinton 1976, Nelson and Mech 1984, Tierson et al. 1985, Nixon et al. 1991). With a few notable exceptions (Nixon et al. 1991) researchers have found considerably higher dispersal rates among male deer, similar to most mammals (Greenwood 1980). While molecular techniques have not previously been applied to dispersal in white-tailed deer, studies with other species show that these techniques are effective at detecting sex-biases even when the bias is not extreme (Mossman and Waser 1999). Goudet et al. (2002) found that all three methods used in this study consistently could detect sex-biased dispersal if the dispersing sex were 4 times more likely to disperse than the philopatric sex and total natal dispersal was >10% of the population. Several studies of white-tailed deer have found sex-based differences in dispersal that were greater than 4 times (Hawkins and Klimstra 1970, Kammermeyer and Marchinton 1976, Tierson et al. 1985). It seems likely that the methods we used would detect bias on the order reported for these populations.

The same factors that contributed to the lack of population subdivision in the SRS deer population could account for our observations regarding sex-biased dispersal. Goudet et al. (2002) noted that as total dispersal increased, subpopulations became less differentiated and it became more difficult to detect sex-biased dispersal. The lack of genetic subdivision in the population implies that a large degree of genetic exchange occurs among the subpopulations. Genetic exchange occurs primarily through movement (emigration and immigration) of individuals between subpopulations. Fine-scale study of the SRS population provided some direct and indirect evidence that dispersal among female deer is elevated (Comer et al. 2005). The lack of cohesive social group structure among SRS females could contribute to a higher rate of female dispersal, as could high rates of orphaning for female fawns (Etter et al. 1995).

One of the evolutionary hypotheses to explain sex-biased dispersal in mammals is competition for mates due to limited access to members of the opposite sex (Dobson 1982). In polygynous species, mate competition among males is presumed to be greater than that among females. This implies a greater incentive for dispersal among males. This is generally the case for deer; however, females in a low density population may have limited access to males during the estrus period. In populations with limited numbers of males, female deer may actively search for males upon onset of estrus (Hölzenbein and Schwede 1989, Labisky and Fritzen 1998). In a radiotelemetry study, D'Angelo et al. (2004) found that 8 of 13 (62%) does at SRS made 24-hr long-distance excursions that were presumably related to onset of estrus. They observed multiple probable breeding excursions separated by approximately 50 days, in 3 of 13 (23%) does, suggesting repeated estrous cycling. These breeding excursions are similar to those reported for other herds and suggest that females at SRS have limited access to males for breeding purposes. They have at least 2 important implications for genetic structure of the deer population. First, they could provide an important mechanism for gene flow among populations that would not be detected by most direct dispersal measures (e.g., mark-recapture studies). Previous studies have found greater differentiation in maternally inherited mtDNA markers than in biparentally inherited nuclear markers (e.g., Purdue et al. 2000). These results are usually interpreted to imply considerably greater dispersal of males than females; however, breeding excursions of the type described would produce a similar pattern. Females making excursions would acquire additional variability in nuclear DNA but not mtDNA. In addition, the limited access to mates implied by female behavior provides a possible explanation for elevated dispersal among females, especially when combined with the limited social structure in the SRS population. Thus, although males may disperse at greater rates than females at SRS, female dispersal occurs sufficiently often to prevent differentiation of subpopulations and consistent detection of sex-bias in dispersal.

Evolutionary Implications

The results of our analyses emphasize the intraspecific variation in social behavior and population structure for white-tailed deer. This plasticity in social behavior and associated characteristics has been noted previously, and may explain the enormous geographic and habitat range occupied by the species (Marchinton and Atkeson 1985). White-tailed deer inhabit a large portion of North and South America, from Canadian boreal forests to Brazilian rain forest (Demarais et al. 2000). An examination of population ecology in different portions of the range shows remarkable variation in social and breeding behavior. For example, in northern temperate areas of the United States, deer exhibit a well defined fall breeding period or "rut" when the majority of females come into estrous synchronously and are bred. In tropical latitudes, breeding occurs year-round (Demarais et al. 2000). Northern deer also make seasonal migrations from winter to summer range and may congregate in large numbers at specific locations (yards) during severe winters. Deer in milder climates do not typically make regular seasonal movements. The primary social organization in forested or mixed habitats is solitary animals or small, single-sex groups but deer in open habitats may associate in small, mixed herds (Hirth 1977).

The results presented here and in Comer et al. (2005) suggest that deer can exhibit plasticity in social behavior in response to differing management histories in addition to differing latitudes or habitats. Because management activities occur over an evolutionarily short time frame (~40 years at SRS), this implies that social behaviors can change rapidly and that deer have a genetic capacity for plasticity. White-tailed deer have higher levels of genetic variation as measured by mean heterozygosity and percentage of polymorphic allozyme loci than other species of ungulates (Baccus et al. 1983, Honeycutt 2000). They also have among the highest levels of variability reported for mtDNA (Purdue et al. 2000). DeYoung et al. (2003) noted that the average allelic diversity at microsatellite loci was considerably higher for white-tailed deer than for Wapiti (*Cervus elaphus*), Japanese sika deer (*C. nippon*), or moose (*Alces alces*). It may be that the capacity for behavioral plasticity itself is adaptive in white-tailed deer by allowing for increased effective population size. The observations of elevated genetic variability could reflect this genetic capacity for variation in behavior.

Implications for Conservation or Management

The behavioral plasticity evident in white-tailed deer implies some caution in applying management strategies based on behavioral or population genetic observations in one population or in a limited part of the species' range. Management strategies for deer have been proposed based on the observations of persistent social structure in New York (Porter et al. 1991, 2004). Our research suggests these strategies may be less effective at the SRS. Furthermore, this phenomenon is not unique to white-tailed deer. For example, Cegelski et al. (2003) found that gene flow in Montana wolverine populations was considerably less than in Alaskan populations, with implications for the acceptable rate of harvest in Montana. In practice, many social and behavioral traits are considered to be static or stable within a given species; however, white-tailed deer provide a clear example of the capacity for variability in these characteristics.

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Table 3.1. Number of white-tailed deer tissue samples obtained for genetic analysis, presented by study area, gender, and age class from the Savannah River Site, Aiken, South Carolina, 2001–2002.

	Adults		Juveniles		
Subpopulation	Male	Female	Male	Female	Total
1	44	34	6	8	92
2	32	36	9	18	95
3	33	36	7	9	85
4	51	41	10	10	112

Table 3.2. Mean number of alleles per locus (A/L), mean allelic richness (AR), mean observed and expected heterozygosity, and number of loci out of Hardy-Weinberg equilibrium (HWE) for 14 microsatellite loci in 4 subpopulations of white-tailed deer at the Savannah River Site, Aiken, South Carolina, 2001–2002.

Subpop	A/L	AR	H_o	H_e	HWE
1	9.9	10.0	0.30	0.29	0/14
2	10.1	9.7	0.31	0.29	0/14
3	9.5	9.5	0.30	0.29	0/14
4	10.1	9.7	0.30	0.28	1/14

Table 3.3. Pairwise F_{ST} values (below diagonal) and *P*-values for subpopulation differentiation based on exact tests (above diagonal) for 4 subpopulations of white-tailed deer at the Savannah River Site, Aiken, South Carolina, 2001–2002.

Subpop	1	2	3	4
1	–	>0.5	>0.5	>0.5
2	0.0121	–	>0.5	>0.5
3	0.0061	0.0075	–	>0.5
4	0.0042	0.0054	0.0041	–

Table 3.4. Results of tests for sex-biased dispersal, including number of individuals, population sex-specific F_{ST}, mean corrected assignment index (AI_c) and variance of AI_c, for white-tailed deer at the Savannah River Site, Aiken, South Carolina in 2001-2002.

			AI_c	
	n	F_{ST}	Mean	Var.
Females	147	0.0054	0.290	**16.13**
Males	160	0.0045	-0.266	**22.56**
P-value[1]		0.418	0.140	**0.048**

[1] Bold type indicates significant results ($P < 0.05$)

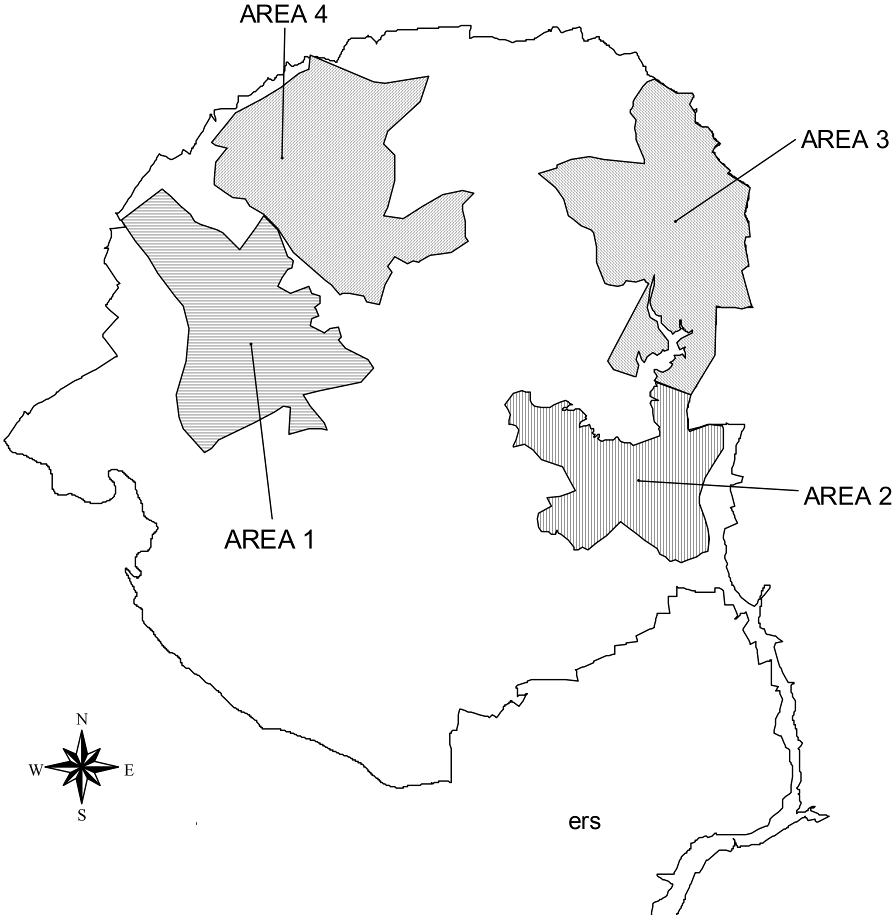

Figure 3.1. Site map of the Savannah River Site, Aiken, South Carolina showing the spatial boundaries of 4 subpopulations for sampling of white-tailed deer in the analysis of population genetic structure in 2001–2002.

CHAPTER 4

POPULATION GENETICS OF WHITE-TAILED DEER AND IMPLICATIONS FOR LOCALIZED MANAGEMENT IN FORESTED HABITATS[3]

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[3] Comer, C. E., J. C. Kilgo, G. J. D'Angelo, T. C. Glenn, and K. V. Miller. To be submitted to *The Wildlife Society Bulletin*.

ABSTRACT

Recently proposed concepts for white-tailed deer (*Odocoileus virginianus*) management rely on assumptions about social and genetic structure. Studies of deer genetic structure have suggested that the existence of persistent matrilineal groups among female deer can lead to the formation of genetically distinct subpopulations. This social and genetic structure may enable managers to create a persistent zone of low deer density in a small area. Using 14 microsatellite DNA loci, we tested for the existence of genetically distinct subpopulations in localized removal areas at the Savannah River Site, Aiken, South Carolina. We removed 134 deer from 4 removal areas and compared their genetic data to 138 deer from surrounding habitats. We used a combination of Bayesian assignment tests, migration rate estimation, and pairwise relatedness estimation to determine the extent to which these removal areas formed genetically distinct subpopulations. Our results provided limited evidence for genetic differentiation of these removal areas from surrounding habitats. Differences in social behavior due to past management history provide the most logical explanation for our results. These results suggest that detailed data on social behavior of a population may be required to ensure the effectiveness of localized management techniques.

Key words: assignment test, localized management, microsatellites, population genetics, *Odocoileus virginianus*, white-tailed deer

INTRODUCTION

In many parts of the eastern United States, white-tailed deer have reached population levels that have negative impacts on society (McShea et al. 1997). These negative impacts can include damage to agricultural crops and landscape plantings, changes in plant community composition and structure (e.g., McShea and Rappole 1997), regeneration failures of commercially harvested timber stands (Alverson et al. 1988, Tilghman 1989), and deer-vehicle collisions. Conover (1997) estimated the total negative impacts from deer at greater than \$2 billion annually in the United States.

The localized management concept proposes that a persistent zone of low deer density can be maintained by removing social groups of female deer from a localized area (Porter et al. 1991). This concept has been suggested as an effective strategy for managing white-tailed deer populations in suburban and forested habitats (Porter et al. 2004, Oyer and Porter 2004). In a test of the concept, McNulty et al. (1997) removed deer from a 3-km^2 area in the Adirondack Mountains, New York. Their results suggested that deer density remained low in the removal area for 5 years following the removal and that deer occupying adjacent habitats did not shift their home ranges in response to the removal (McNulty et al 1997, Oyer and Porter 2004).

The localized management concept is based on assumptions about social and genetic structure in white-tailed deer (Porter et al. 1991). It assumes that female deer associate in persistent matrilineal groups consisting of several generations of related does (Tierson et al. 1985). The concept also assumes that female offspring exhibit a high degree of philopatry, forming a home range that overlaps that of their dam (Hawkins and Klimstra 1970, Aycrigg and Porter 1997). Individual home ranges within the group overlap but matrilineal groups occupy geographically distinct ranges (Aycrigg and Porter 1993). Genetic structure in the deer herd is therefore central to the population model underlying the localized management concept (Mathews and Porter 1993). Mathews and Porter (1993) found that matrilineal social groups in the Adirondacks were genetically distinct based on allozyme analysis and concluded that they consisted of closely related animals.

Previous genetic studies of white-tailed deer using allozymes or mitochondrial DNA restriction fragment analysis have suggested the presence of genetic structure at landscape or regional scales (Kennedy et al. 1987; Ellsworth et al. 1994a,b; Leberg et al. 1994, Leberg and Ellsworth 1999). Purdue et al. (2000) found evidence for female philopatry and spatial heterogeneity in southeastern deer populations using mitochondrial DNA and allozyme analysis. The discriminatory power of allozyme and restriction fragment techniques at the scale of the matrilineal group is limited by their low allelic or haplotype diversity. However, microsatellite DNA markers can be used to estimate relatedness between pairs of individuals or discriminate among closely related populations (Paetkau et al. 1995, Blouin 2003). The recent development of microsatellite markers for white-tailed deer by Anderson et al. (2002) provides the opportunity to examine genetic structuring at smaller spatial scales.

We analyzed microsatellite DNA loci to determine if genetically distinct subpopulations exist in localized removal areas at the Savannah River Site (SRS) in South Carolina. The SRS has a history of intensive white-tailed deer management in an effort to reduce the incidence of deer-vehicle collisions (Novak et al. 1999). However, sitewide reductions in deer density have not resulted in equivalent reductions in collision rates (Novak et al. 1999). Previous studies suggested the presence of genetically distinct subpopulations in SRS deer. Ramsey et al. (1979) found that deer at the SRS were genetically segregated by habitat type, and Scribner et al. (1997) observed significant spatial and temporal genetic clustering. Thus, a program was initiated in 2001 to determine the feasibility of localized management to more effectively manage the SRS population (Johns and Kilgo in press). The current study was conducted to evaluate the localized management program to determine if genetic characteristics of the population were consistent with the predictions of the localized management concept.

STUDY AREA

The SRS is an approximately 800-km^2 National Environmental Research Park encompassing portions of Aiken, Barnwell, and Allendale Counties, South Carolina. The SRS is owned by the U.S. Department of Energy (DOE) and managed jointly by DOE and Westinghouse Savannah River Company (WSRC), Inc. While active facilities occupy portions of the site, most of the SRS is undeveloped. The SRS is within the upper Coastal Plain physiographic province. It is approximately 68% pine forest, consisting primarily of variable-aged stands of longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine (Imm and McLeod in press). Swamps and riparian bottomlands dominated by hardwoods, including oaks (*Quercus* spp.), sweetgum (*Liquidambar styracifolia*), and blackgum (*Nyssa sylvatica*), occupy 22% of the site. Upland hardwoods, including oaks and hickories (*Carya* spp.), represent approximately 7% of land cover. Forested stands are interspersed with open habitats such as powerline rights-of-way, recent timber harvests, and road/facilities areas.

The deer herd at SRS has been managed since 1965 by annual dog-drive deer hunts over much of the site. Current population density varies across the site but generally is estimated at 4–6 deer/km^2 in most areas (Novak et al. 1999). Despite the low deer density, deer-vehicle collisions are considered a management problem. From 1992–2000, the SRS averaged 98 deer-vehicle collisions annually (Johns and Kilgo in press).

For this study, we selected 3 study areas in the upland portion of the SRS (Fig. 4.1). Study areas were centered on major site roadways with historically high deer-vehicle collision rates. Each area was approximately 1,800 ha and consisted of a 3-km buffer around the central roadway for a distance of approximately 6 km of road. Areas 2 and 3 were entirely undeveloped at the time of the study while Area 1 consisted of forested habitats interspersed with site industrial facilities. Vegetative cover in undeveloped portions of all three study areas was typical of upland portions of the SRS.

METHODS

Removals

Removal actions were implemented on all 3 study areas in fall 2001 and winter 2002. Removal methods varied among the three areas and consisted of a combination of targeted roadside dog hunts and sharpshooting by project personnel. Dog hunts were conducted under the oversight of WSRC personnel and were specifically planned to hunt the 3-km-wide removal area corridor. Each hunt included approximately 50 dog packs, each accompanied by 2 hunters, and an additional 20 stationary stand hunters. All dog release points and stationary stands were within the 3-km corridor. Sharpshooting consisted of nightly spotlighting and shooting all deer within a smaller 1-km corridor surrounding the central roadway. Specific removal methods for each of the 3 removal areas in fall 2001 and winter 2002 were as follows: in Area 1, 2 dog hunts (17 November 2001, 1 December 2001); in Area 2, 2 dog hunts (8 December 2001, 15 December 2001);

and in Area 3, 1 dog hunt (24 November 2001) followed by sharpshooting from 27 November 2001–1 March 2002.

Due to concerns that 2001 removals in Area 1 did not meet site management objectives, further removals were implemented in this area in fall 2002. The treatments were dog hunts identical to those in 2001, and consisted of 2 hunts (12 October 2002 and 19 October 2002). We conducted no additional removals in Areas 2 or 3 during 2002.

We collected an approximately 20-cm^3 piece of abdominal muscle for genetic analysis from all deer killed during removals. Hunters were interviewed immediately after all dog hunts to ensure that deer were killed within the 3-km removal corridor. Tracking of radio-marked deer during management hunts found that deer generally remain within or near the boundary of their seasonal home range during hunts (D'Angelo et al. 2003); therefore, the locations of hunter-killed deer are representative of their typical range. In addition to the removal deer, we obtained muscle tissue samples from all deer killed by vehicle collisions on roads within removal areas from April 2001 through December 2002.

Background Samples

To determine if removal areas formed genetically distinct subpopulations from surrounding areas, we sampled deer from adjacent habitats for comparison. These background samples were from hunt units immediately adjacent to the removal areas (Fig. 4.2), so that each set of removal area samples had a corresponding set of background samples. We obtained background samples from deer killed in standard management hunts between 23 October 2002 and 11 December 2002. Standard management hunts are conducted over large areas (>30 km^2) and generally avoid major road corridors. We collected muscle tissue samples from all deer killed in management hunts in appropriate hunt units using a procedure identical to that used for removal area samples. We then randomly selected samples from among those available to analyze and use for comparisons. By sampling deer from all hunt units adjoining the removal areas, we were able to obtain a representative estimate of genetic variability in the population immediately surrounding the removal areas.

Microsatellite Analyses

Tissue samples were frozen and stored at -70° C until DNA extraction. We extracted DNA from tissue samples using Qiagen DNEasy DNA isolation kits (Qiagen, Inc., Valencia, CA, USA). Following extraction, we quantified DNA concentration in the resulting solution by 1% agarose gel electrophoresis with ethidium bromide staining, using lambda DNA for reference (Sambrook et al. 1989).

Anderson et al. (2002) identified 21 polymorphic microsatellite loci in white-tailed deer from Oklahoma. Based on analyses of 80 randomly chosen individuals from SRS, 14 of these loci were determined to be polymorphic and did not deviate significantly from the expectations of Hardy-Weinberg equilibrium (C. E. Comer, University of Georgia, unpublished data). Following DNA isolation, we used polymerase chain reaction (PCR) to amplify these 14 microsatellite loci using primers and reaction conditions described by Anderson et al. (2002). After amplification, PCR products were loaded onto 12-cm acrylamide microsatellite gels and electrophoresed in an ABI 377 analyzer (Applied Biosystems, Inc., Foster City, CA, USA). To aid in distinguishing loci, primers were fluorescently labeled with 1 of 3 dyes (NED, FAM, or HEX) as identified in Anderson et al. (2002). An internal size standard (R-500, Genetix, New Milton, U.K.) was also loaded with each sample to allow size identification of microsatellite alleles. Chromatograms derived from microsatellite runs were analyzed initially with GENESCAN (Applied Biosystems, Inc. Foster City, CA, USA), and then imported into GENOTYPER 2.5 (Applied Biosystems, Inc. Foster City, CA, USA) for characterization of alleles. We used the web version of GENEPOP (Raymond and Rousset 1995) to evaluate whether each of our loci was at Hardy-Weinberg equilibrium (HWE) in the population tested and the program CERVUS 2.0 (Marshall et al. 1998) to calculate the polymorphic information content (PIC) of each locus. We used sequential Bonferroni correction to account for multiple tests in the HWE calculations (Rice 1989).

Data Analysis

We assessed the degree of genetic differentiation of the removal areas using a combination of tests for subpopulation differentiation, immigration rate estimation, and relatedness calculations. Because the population models underlying the localized management concept predict greater genetic structure and differentiation among female deer, we also conducted all analyses separately on 2 data sets. The first included all deer sampled to assess genetic structure in the entire population and the second included only females.

To test subpopulation differentiation, we used a combination of methods based on F_{ST} (Wright 1978) and methods based on assignment tests (Paetkau et al. 1995). For the former analysis we calculated pairwise values of both F_{ST} and its analog R_{ST} (Slatkin 1995). Although R_{ST} is based on a stepwise mutation model that may be more appropriate for microsatellite DNA loci, empirical testing has shown that F_{ST} may be more appropriate when gene flow is relatively high (Balloux and Goudet 2002). For F_{ST}

calculations, we used the unbiased estimator of Weir and Cockerham (1984) as implemented in the program FSTAT (Goudet 2001). We used the algorithm in the program RSTCALC to estimate R_{ST} values (Goodman 1997). For both estimators we used permutation tests as implemented in the respective programs to test for significance of the results. We used sequential Bonferroni correction to account for multiple comparisons (Rice 1989).

Assignment test methods calculate genetic differentiation between populations by using allele frequencies in potential source populations to allocate individuals among those populations based on individual genotype data (Hansen et al. 2001). The percentage of individuals assigned correctly is directly related to the degree of differentiation between the potential source populations. DeYoung et al. (2003a) found that the white-tailed deer microsatellite loci developed by Anderson et al. (2002) assigned 94% of deer in Texas and Mississippi to their correct population of origin. We performed assignment tests using the computer program GeneClass 2.0.b (Cornuet et al. 1999). Several assignment algorithms are available in GeneClass, but we used the Bayesian likelihood approach modified from Rannala and Mountain (1997) because data simulation has shown it consistently performs better than other methods (Cornuet et al. 1999). We did all assignment tests in pairwise fashion, comparing a removal area population to the background population from immediately adjacent hunt units.

The rate at which deer disperse from adjacent habitats into a removal area is an important limiting factor in the potential success of the localized management concept (Porter et al. 2004). Recently derived statistical procedures allow the estimation of immigration rates among populations based on multilocus genotype data (Pritchard et al.

2000, Wilson and Rannala 2003). We used the Bayesian likelihood approach in the computer program BayesAss 1.2 to estimate immigration rates between removal areas and adjacent background populations (Wilson and Rannala 2003).

For the third analysis, we used a relatedness approach rather than a genetic differentiation approach. The localized management concept is based on the existence of persistent matrilineal groups of female deer within the removal area. If these matrilineal groups were present in the removal areas in this study, we would expect to see a higher degree of relatedness among deer from the removal areas compared to that among deer from the larger, more variable hunt units adjacent to the removals. Microsatellite data can be used to accurately assign pairs of individuals to relationship categories (Blouin 2003). The program Kinship 1.2 uses a likelihood ratio approach to test hypotheses regarding the pedigree relationships among pairs of individuals (Queller and Goodknight 1989). By simulating many hypothetical pairs based on population allele frequencies, the program also provides statistical confidence in these assignments (Queller and Goodknight 1989). We used Kinship 1.2 to determine the percentage of deer pairs in each population that are 2nd degree related or closer. This degree of relationship is consistent with a half-sibling, grandparent-grandchild, or avuncular relationship (Blouin 2003). We used χ^2 tests to determine if the percentage of 2nd-degree related deer pairs was higher than expected in the removal areas. We applied sequential Bonferroni correction to these data to account for multiple tests (Rice 1989). We also used a *t*-test for paired samples to compare the percentage of related pairs in removal areas to that in background areas. We applied an arcsine square root transformation to the data prior to implementing the *t*-test (Dowdy and Weardon 1991). We used SAS for statistical calculations (SAS Institute, Cary, North Carolina, USA).

RESULTS

During the period from April 2001 to December 2002, we obtained tissue samples from 134 white-tailed deer from the 3 removal areas (Table 4.1). These included 74 females and 60 males. During this same period, we sampled 138 deer (67 females and 71 males) from background locations in hunt units adjacent to the removal areas (Table 4.1).

Microsatellite Analysis

We observed a high degree of diversity in the microsatellite loci used for this study (Table 4.2). Based on all 272 individuals sampled, the number of alleles ranged from 3–22 with a mean of 10.9. Observed heterozygosity ranged from 0.401–0.863 with a mean of 0.694. The mean PIC was 0.679 with a range of 0.360–0.892. Overall, these values are similar to those reported for the same microsatellite panel by DeYoung et al. (2003a), although the characteristics of individual loci varied substantially. We found 4 loci (BM4208, BM6506, ETH152, and N) that had $P < 0.05$ for the test of HWE; however, none exceeded the threshold *P*-value after Bonferroni correction for multiple tests. An advantage of the Bayesian algorithms used for assignment tests and migration rate estimation is that the assumption of HWE is relaxed, so we retained all 14 loci for our genetic analyses.

Subpopulation Differentiation

The F_{ST} and R_{ST} values for pairwise comparisons of removal and background areas suggested little differentiation in most areas (Table 4.3). None of the removal and background areas were genetically different based on R_{ST} values. However, the F_{ST}

values calculated for Area 2 were significantly different from 0 by permutation tests, suggesting some degree of differentiation in this removal area for both all deer and females only.

The results of assignment tests are expressed as the percentage of individuals that were assigned to the correct population based on genetic information. These results should be considered relative to a random assignment of individuals among the potential source populations. For the analyses presented here, randomly assigning individuals between populations would result in 50% of individuals assigned correctly. For comparisons using both male and female deer, the percentage of deer assigned correctly between removal areas and background hunt units varied from 52–71% in the 3 removal areas (Fig. 4.3). Using only female deer, GeneClass was able to correctly assign 52–74% of individuals to the correct population. Area 2 had the highest percentage of deer assigned correctly when only does were considered, while Area 1 had the highest percentage when all deer were considered.

Migration Rates

The mean rate of migration from background populations into removal area populations varied from 3–32% per generation for all deer and from 4–32% per generation for females only (Fig. 4.4). The BayesAss program has an upper limit of 33% on migration rate built into the program, so estimated migration rates near this level may reflect actual migration rates that are somewhat higher (Wilson and Rannala 2003). Estimated migration rates for does were similar to those for all deer in Removal Areas 1 and 3; however, the migration rate estimate for does was much lower than that for all deer in Removal Area 2.

Relatedness

We set the parameters of the Kinship program such that the threshold for rejecting the null hypothesis of no relationship was $P = 0.05$. This threshold indicates the probability that a pair is incorrectly assigned to the 2nd-degree related category when the deer are in fact unrelated (i.e., a Type I error). Because of this conservative threshold, the chance of a Type II error for our analysis was 0.29 indicating that some related pairs were misclassified as unrelated. However, the Type II error rate was similar for all analyses, and comparisons were still valid between removal and background areas.

Our analysis revealed no significant deviations from the expected distribution of related pairs after Bonferroni correction for multiple comparisons (Table 4.4). We observed the greatest differences between removal and background areas in Area 3. The results of paired *t*-test confirmed that overall the percent related pairs in background areas did not differ from removal areas for all deer ($n = 3$, $t = -0.65$, $P = 0.58$) or does only ($n = 3$, $t = 0.83$, $P = 0.49$).

DISCUSSION

Our data did not support the concept that social behavior induced the formation of genetically distinct subpopulations among deer at SRS. The social ecology of white-tailed deer provides a mechanism for the development of genetic structure. The formation of matrilineal groups consisting of several generations of related females may limit dispersal and gene flow (Hawkins and Klimstra 1970, Mathews and Porter 1993). Several studies have shown differentiation of white-tailed deer populations across landscape and regional scales using both mitochondrial and nuclear DNA markers (Purdue et al. 2000, DeYoung et al 2003b). However, management strategies have been proposed for this species based on the existence of genetic structure at a smaller spatial scale—that of the social group (Porter et al. 2001). The study by Mathews and Porter (1993) of white-tailed deer in the Adirondack Mountains provides the only study of genetic structure among deer at this small spatial scale. They identified social groups using radiotelemetry and visual association of marked individuals. Using primarily Wright's F_{ST} (Wright 1978) analysis of allozyme data, they found that these social groups were genetically distinct units. Our results suggest that genetic structure at this scale is not ubiquitous in white-tailed deer populations.

Deer from localized management removal areas did not exhibit a high degree of genetic differentiation compared to deer from adjacent, background habitats. The F_{ST} values for Area 2 were different from 0, suggesting that these populations are not genetically identical. However, values of $F_{ST}<0.05$ generally indicate little genetic differentiation between populations (Wright 1978). Interpretation of low values of F_{ST} can be difficult (Balloux and Lugon-Moulin 2002). Assignment tests showed that the maximum successful assignment rate was less than 75%. Considering that random allocation of individuals with no genetic information would provide a 50% rate of correct assignment, this does not represent a high degree of differentiation. Interestingly, the results of calculations including only females did not suggest greater differentiation than males and females combined. Purdue et al. (2000) found that maternally inherited markers displayed much more spatial heterogeneity than biparentally inherited markers in several southeastern populations, including the SRS. The smaller sample sizes for comparisons involving only females may be partially responsible for our results, but there are also important differences in scale between the two studies. Purdue et al. (2000)

considered multiple sites across Georgia and South Carolina that were separated by >25 km. The entire 800-km^2 SRS was considered a single sample location. Nonetheless our results are surprising in light of currently accepted models of social structure in deer.

Overall, immigration rates suggest that extensive exchange of individuals occurs between the removal areas and background areas. An exception was in Area 1, where estimated rates of immigration were less than 5% per generation. Due to the interspersion of developed facilities and forested habitats in and around the removal area, this was the least precisely defined removal area. Because the opportunity to remove deer from the vicinity of developed facilities is limited, it is likely that significant segments of the population around Area 1 remained unsampled for this analysis. This was true for the 3-km wide removal area and, even more, for the background habitats. Based on this, it is likely that immigration into the removal area occurs from locations that we were not able to sample. The BayesAss algorithm considers only the sampled populations as potential sources of immigrants, so our analysis may have underestimated immigration rate in Area 1. The results of assignment tests for Area 1 support this conclusion, as the ability to assign deer to background and removal populations was essentially equal to a random assignment. Another exception was the rate of immigration among female deer in Area 2. In combination with the F_{ST} and assignment test results, these suggest that a slightly greater degree of genetic structure was present in this area compared to the other 2 areas.

The Kinship analysis suggested that there was little genetic structure in our study areas. This analysis used a different analytical approach to examine genetic structure in the deer population. Rather than testing for genetic differentiation, these analyses tested for the evidence of matrilineal groups within the removal area. If matrilineal groups were present, we expected to see greater incidence of closely related deer pairs in the removal areas compared to the more widely dispersed samples from the background areas. We observed a greater percentage of related pairs in the removal area than in the background area in Area 3; however the differences were not significant and we observed no such relationship in the other 2 areas.

We found limited evidence for genetic differentiation of subpopulations at the scale of the social group considered in this analysis. While evidence suggested some degree of genetic and social structure in Area 2, we did not see the genetic subdivision observed by Mathews and Porter (1993) and used to support the localized management concept (McNulty et al. 1997).

The differences between our results and those of previous studies may be due to differences in the design of our removals or due to social or behavioral differences between the two deer herds. In their test of the localized management concept in the Adirondacks, McNulty et al. (1997) identified a social group of 17 female deer and targeted the social group for removal. This resulted in a removal area of 1.4 km^2, although 3 target deer were not removed from the periphery of the area. Our removal areas were defined geographically by proximity to target roadways with no prior knowledge of the social structure. We designed the removal areas in this manner because we were interested in the feasibility of localized management in reducing deer-vehicle collisions. Our design undoubtedly led to the partial removal of some social groups and may have obscured genetic distinctions between removal and background areas. However, practical application of the localized management concept requires that removal areas be defined without detailed knowledge of deer social structure (McNulty et al. 1997). Our 1,800-ha removal areas were considerably larger than the cumulative social group ranges of 160–720 ha in the Adirondacks (Mathews and Porter 1993), so entire social groups, if present, would be within the removal areas. In any case, the social model underlying the localized management concept implies that deer within a smaller, continuous area (the removal area) should be more genetically similar than those in a larger, dispersed area (background area). It also implies that greater differentiation would be observed among does than among deer of both genders. Therefore, we believe that the differences in design do not fully account for our observations and that some further explanation is necessary.

The logical alternative explanation is that social behavior among deer at the SRS is different from that observed in the Adirondacks. In a study of deer at SRS using radiotelemetry and genetic data, Comer et al. (2005) found that closely related does did not form persistent, cohesive social groups. As noted there, the heavy annual harvest of female deer at SRS (~25% of does available) has created a younger age structure where less than 4% of harvested does are >5 years old. There is some evidence that female dispersal rates also may be elevated (Comer et al. 2005). Aycrigg and Porter (1997) found little spatial structure among does <5 years old in the Adirondacks, and Porter et al. (2004) noted that high rates of dispersal among does could limit the formation of cohesive social structure and the effectiveness of localized management.

We found evidence for limited genetic differentiation and structure at the scale of interest among SRS deer; however, it appears that harvest history and perhaps other behavioral factors have prevented extensive genetic differentiation at the scale of the social group in this population. These results do not necessarily contradict evidence of genetic structure at state or regional (e.g., Purdue et al. 2000, DeYoung et al. 2003b) or landscape (e.g, Scribner et al. 1997) scales; however, they call into question some commonly accepted models of white-tailed deer population structure at the level of the social group.

MANAGEMENT IMPLICATIONS

Management strategies based on social structure in white-tailed deer populations have the potential to address problems of overabundant deer populations. The localized management concept developed by Porter et al. (1991) and tested by McNulty et al. (1997) and Oyer and Porter (2004) has been proposed as an efficient method for controlling deer populations in a small area. The appeal of this approach is evident in the number of recent publications suggesting it as a solution to suburban deer problems (Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004). However, our data suggest that such recommendations should not be made without detailed data on social structure in the managed population.

This study examined the assumptions of social and genetic structure that provide the basis of the localized management concept. Our data indicate that, in the SRS population, limited genetic differentiation of subpopulations was present at the level of the social group described by Mathews and Porter (1993). The elevated immigration rates present in the population are of particular concern for the localized management concept. According to Porter et al. (2004), dispersal of female deer represents an important limiting factor in the effectiveness of localized management. We observed up to 32% migrants per generation among deer in the removal areas. In a localized management situation, migrant individuals are potential colonizers of habitats where deer have been removed. A review of the dispersal literature reveals a high degree of plasticity in female dispersal rates for white-tailed deer, from <5% (Aycrigg and Porter 1997, Campbell 2004) to ≥20% (Nixon et al. 1991, Nelson and Mech 1992). In view of this plasticity in behavior and the results of the current study, the expected degree of success is uncertain in applications of localized management to areas where white-tailed deer social behavior is poorly understood.

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Table 4.1. Numbers and method of sampling for white-tailed deer sampled for removal treatments at 3 road areas on the Savannah River Site, Aiken, South Carolina in 2001–2002.

		Number Sampled/Removed		
Road Area	Sample Type	Males	Females	Total
1	2001 Dog Hunts	7	5	12
	2002 Dog Hunts	12	9	21
	Roadkill	5	5	10
	Background	26	23	49
2	2001 Dog Hunts	17	26	43
	Roadkill	0	2	2
	Background	24	26	50
3	2001 Dog Hunts	7	6	13
	Sharpshooting	9	21	30
	Roadkill	3	0	3
	Background	21	18	39

Table 4.2. Locus name, number of alleles, observed heterozygosity, expected heterozygosity, *P*-value for deviation from Hardy-Weinberg equilibrium (HWE), and polymorphic information content (PIC) for 14 microsatellite DNA loci genotyped for 272 white-tailed deer from the Savannah River Site, Aiken, South Carolina, 2001-2002.

		Heterozygosity			
Locus[a]	Alleles	Observed	Expected	HWE *P*-value	PIC
BL25	6	0.622	0.667	0.383	0.620
BM4208	20	0.863	0.901	0.009	0.892
BM6506	13	0.819	0.836	0.008	0.817
BovPRL	3	0.507	0.526	0.711	0.416
Cervid1	14	0.831	0.827	0.343	0.805
D	10	0.822	0.840	0.591	0.821
ETH152	11	0.783	0.828	0.012	0.806
INRA011	6	0.585	0.594	0.813	0.554
K	6	0.444	0.436	0.142	0.388
N	21	0.787	0.883	0.012	0.872
O	6	0.401	0.439	0.146	0.360
OarFCB193	13	0.621	0.564	0.476	0.546
P	8	0.790	0.769	0.634	0.733
Q	16	0.846	0.885	0.391	0.873

[a] Locus names from Anderson et al. (2002).

Table 4.3. Pairwise values for genetic differentiation (F_{ST} and R_{ST}) for white-tailed deer sampled from removal and background areas at the Savannah River Site, Aiken, SC, 2001-2002. Values in bold were significantly different from 0 ($\alpha = 0.05$) after sequential Bonferroni correction for multiple tests.

	All Deer		Females Only	
Area	F_{ST}	R_{ST}	F_{ST}	R_{ST}
1	0.0009	0.0003	-0.0020	-0.0007
2	**0.0041**	0.0082	**0.006**	0.0148
3	0.0037	-0.0059	-0.0011	0.0010

Table 4.4. Number of total deer pairs (*n*), percent of pairs related at 2^{nd} degree or greater (% Rel), and results of χ^2 tests for deviations from expected values for comparisons between removal and background areas for 3 study areas at the Savannah River Site, Aiken, South Carolina in 2001–2002.

		Removal		Background		Comparison	
Area	Data Set	*n*	% Rel	*n*	% Rel	χ^2	*P*
1	All Deer	903	6.9	1176	8.6	2.10	0.148
	Females	171	9.9	253	6.7	1.44	0.231
2	All Deer	990	10.2	1225	10.0	0.036	0.850
	Females	378	8.7	325	12.0	2.03	0.154
3	All Deer	1035	10.7	741	7.7	4.64	0.031
	Females	351	14.0	153	6.5	5.68	0.017

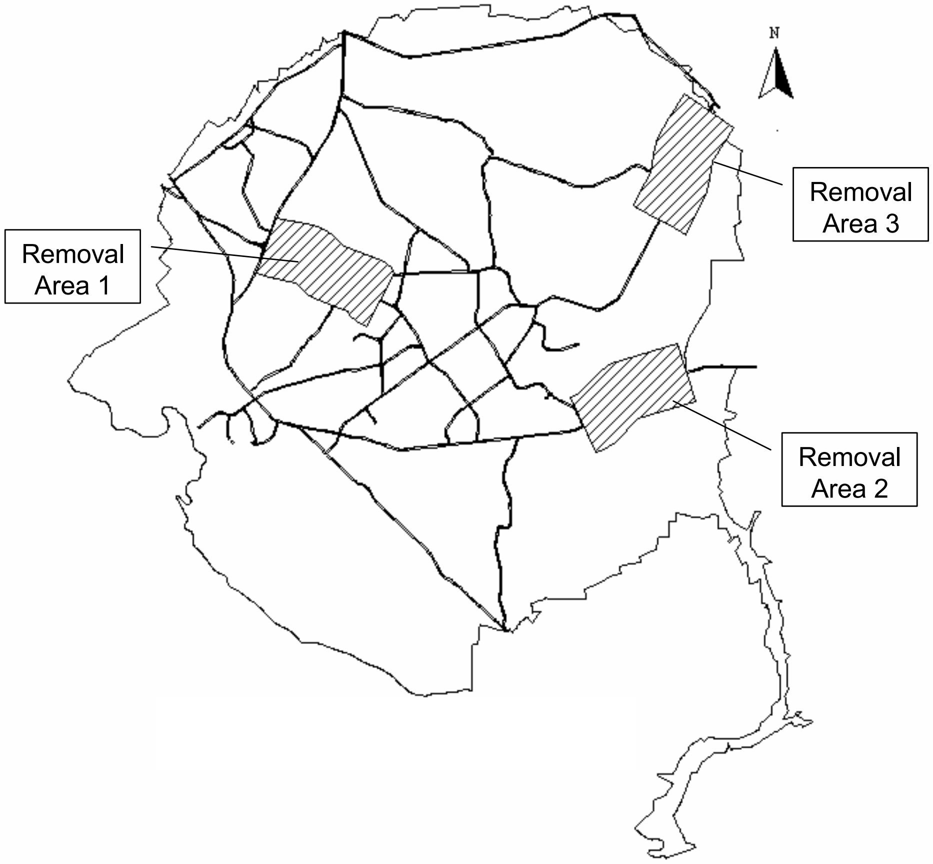

Figure 4.1. Site map of the Savannah River Site, Aiken, South Carolina showing the locations of 3 road corridor study areas to which deer removal treatments were applied in 2001 and 2002.

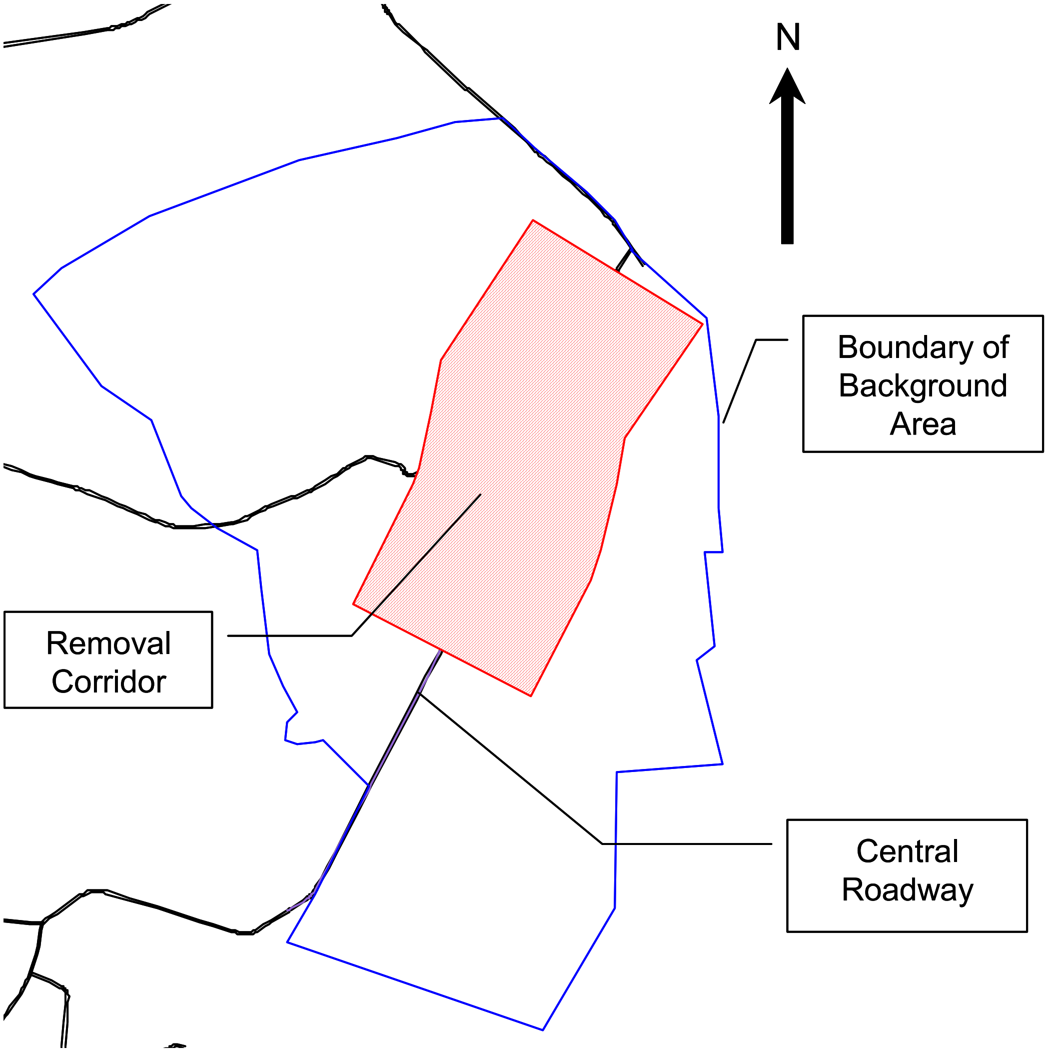

Figure 4.2. Schematic map of Study Area 3 at the Savannah River Site, Aiken, South Carolina, showing central roadway and boundaries of removal and background areas used for white-tailed deer sampling, 2001–2002.

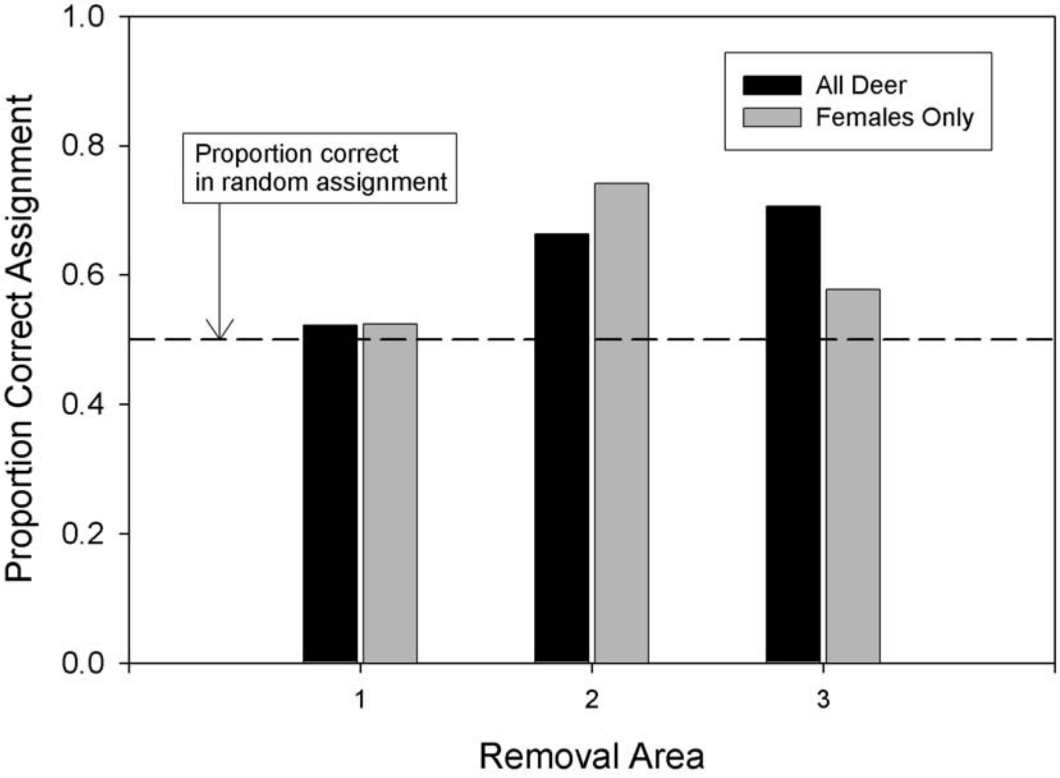

Figure 4.3. Percentage of white-tailed deer correctly assigned to their population of origin between removal areas and adjacent background habitats for 3 Areas at the Savannah River Site, Aiken, South Carolina in 2001 and 2002.

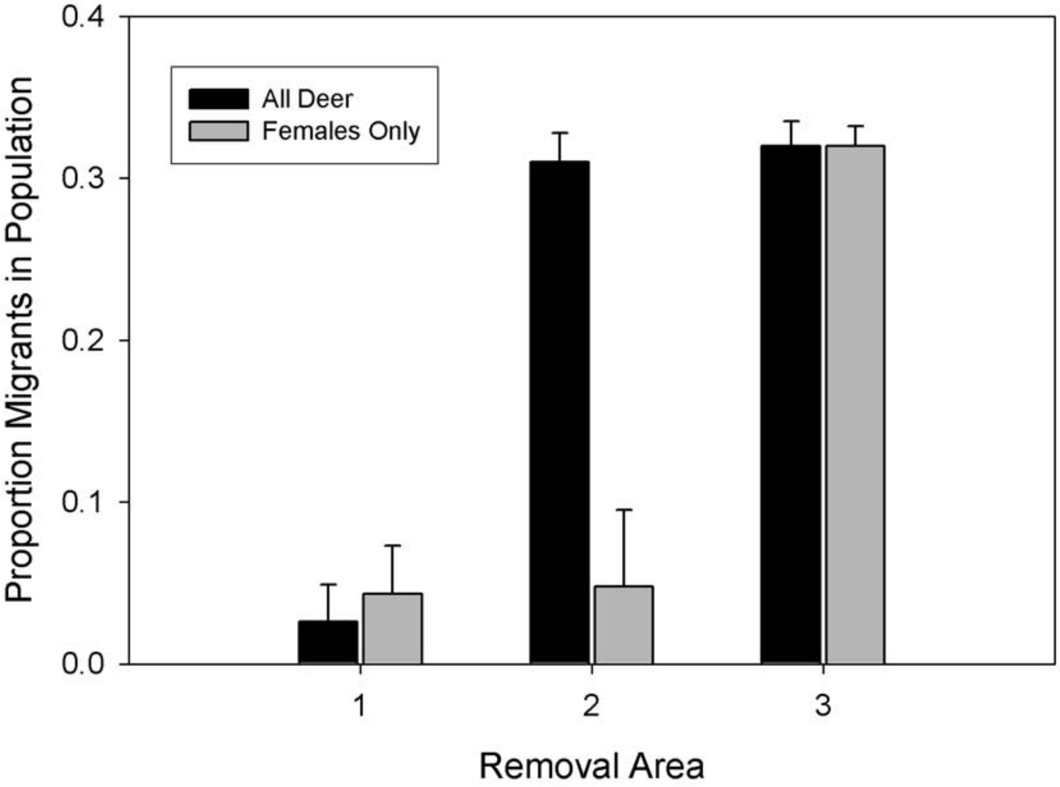

Figure 4.4. Proportion of white-tailed deer in 3 removal area populations that are migrants from adjacent background habitats as estimated by population genetic analysis of deer from the Savannah River Site, Aiken, South Carolina in 2001 and 2002. Bars indicate standard deviation of estimates.

CHAPTER 5

AN EXPERIMENTAL TEST OF LOCALIZED MANAGEMENT IN A LOW-DENSITY WHITE-TAILED DEER POPULATION[4]

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[4] Comer, C. E., G. J. D'Angelo, J. C. Kilgo, and K. V. Miller. To be submitted to the *Wildlife Society Bulletin*.

ABSTRACT

The localized management concept of deer management has been suggested as an effective solution to problems of white-tailed deer (*Odocoileus virginianus*) overabundance in forested and suburban habitats. Field tests to date have shown promising results but have been limited in number and scope. We implemented a field test of localized management in an intensively managed deer population at the Savannah River Site in the upper Coastal Plain of South Carolina. Using combinations of targeted dog hunts and sharpshooting, we removed deer from 4 1,800-ha corridors along major roadways. All removal methods were effective, removing 32–60% of the estimated deer population in the removal areas. Results of pellet group counts, infrared-triggered camera counts, and track counts suggested that abundance of deer in the removal areas was reduced 2 years after treatment. We observed no change in the spatial distribution of deer density in response to the removals. Our results provide general support for the effectiveness of localized management on large (>10 km^2) areas for a period of 2 years. However, our results suggest that the concept may not be effective in small areas or for longer time periods at SRS, thereby emphasizing the need to consider the social and behavioral plasticity of this species in any management decisions.

Key words: localized management, *Odocoileus virginianus*, population indices, Savannah River Site, South Carolina, white-tailed deer

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) populations in many parts of the eastern United States have had negative economic and ecological consequences (McShea et al. 1997), including damage to agricultural crops and landscape plantings, changes in plant community composition and structure (e.g., McShea and Rappole 1997), regeneration failures of commercially harvested timber stands (Alverson et al. 1988, Tilghman, 1989), and deer-vehicle collisions. Conover (1997) estimated negative impacts from deer at more than $2 billion annually, of which the largest component was approximately $1 billion in damages from deer-vehicle collisions. Although precise estimates of the monetary cost of deer-vehicle collisions vary (Schwabe and Schuhmann 2002), there can be little doubt that the issue is a significant and growing problem facing wildlife managers (Romin and Bissonette 1996).

A wide variety of techniques have been used in efforts to reduce the incidence of deer-vehicle collisions, with limited success. Methods tested have included lighted signs (Pojar et al. 1975), warning whistles (Romin and Dalton 1992), highway fences (Falk et al. 1978), crosswalks (Lehnert and Bissonette 1997), and highway reflectors (Reeve and Anderson 1993). A variety of population control or reduction programs have also been implemented to reduce deer-vehicle collisions and other negative impacts (Warren 1997). Although various methods of lethal population reduction are effective, applying these control measures over large areas can be expensive and time-consuming (Doerr et al. 2001).

The localized management concept for deer population control suggests a more efficient technique to reduce negative impacts from deer in a limited geographical area (Porter et al. 1991). This concept relies on several assumptions about white-tailed deer social ecology, and predicts that localized areas of reduced population density may persist without further control for 10–14 years following a single removal (Porter et al. 1991). If effective, localized management presents an appealing option for white-tailed deer management and it has been suggested for control of deer populations in urban and suburban areas (Kilpatrick and Spohr 2000, Porter et al. 2004) and in recently harvested timber stands (Campbell et al. 2004).

Despite its potential for maintaining reduced deer populations in many situations, field tests of the localized management concept are limited to a single removal experiment in the Adirondack Mountains of New York. McNulty et al. (1997) removed 14 white-tailed deer from a 1.4-km^2 area in mountainous, forested habitat. Although the study area was unhunted, deer density was low (2–6 deer/km^2) throughout the study period (Oyer and Porter 2004). Two years after the initial removals, McNulty et al. (1997) observed no movement of radiocollared deer into the removal area. Capture rates and visual observations suggested that deer density had been reduced. Oyer and Porter (2004) examined the same removal area approximately 6 years post-removal and found that radiocollared deer from adjacent habitats did not move into the removal area in that time. Although deer density in the entire research area declined markedly during the 6-year period, abundance within the removal area remained reduced relative to surrounding habitats (Oyer and Porter 2004).

We conducted a field test of the localized management concept in a low density, intensively managed, southeastern deer population at the Savannah River Site (SRS) in South Carolina. Despite low sitewide deer density, the number of deer-vehicle collisions at SRS is unacceptably high from a management perspective (Johns and Kilgo in press). Annual deer hunts provide a locally important recreational resource that could be affected by further reductions in sitewide deer density; therefore, localized management in the vicinity of high-priority roadways could be an effective option. Beginning in fall 2001, we performed experimental removals in 4 corridors surrounding major roadways on SRS. We measured deer abundance and distribution within the removal areas pre-removal and for 2 years post-removal. Our objective was to evaluate the potential effectiveness of localized removals in reducing deer abundance in road corridors while maintaining higher deer density outside the removal areas.

STUDY AREA

The Savannah River Site (SRS) is about 800-km^2, encompassing portions of Aiken, Barnwell, and Allendale Counties, South Carolina. It is a National Environmental Research Park administered by the U.S. Department of Energy (DOE) and managed jointly by DOE and Westinghouse, Inc. While active facilities occupy portions of the site, most of the SRS is undeveloped.

The SRS is located within the Upper Coastal Plain physiographic province. It is approximately 68% pine forest, consisting primarily of variable-aged stands of longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine (Imm and McLeod in press). Swamps and riparian bottomlands dominated by hardwoods, including oaks (*Quercus* spp.), sweetgum (*Liquidambar styracifolia*), and blackgum (*Nyssa sylvatica*), occupy 22% of the site. Upland hardwoods, including oaks and hickories (*Carya* spp.), represent approximately 7% of land cover. Forested stands are interspersed with open habitats such as powerline rights-of-way, recent timber harvests, and road/facilities areas.

The deer herd at SRS has been managed since 1965 by annual dog-drive deer hunts over much of the site. Standard management hunts are large-scale hunts, covering more than 25 km^2 and involving >70 dog packs (with 2 handlers each) and 100–200 stationary stand hunters. The management hunt program typically results in an annual kill in excess of 1,000 deer. The program has successfully maintained the sitewide population near the management target of 4,000 deer, but has not produced a concomitant reduction in deer-vehicle collision rates (Johns and Kilgo in press). From 1990–2000, the SRS averaged approximately 75 deer-vehicle collisions annually (Novak et al. 1999).

We selected 4 study areas in the upland portion of the SRS for the experimental removals. Removal areas were centered on major site roadways with historically high deer-vehicle collision rates. Each removal area was approximately 1,800 ha and consisted of a 3-km buffer around the central roadway for a distance of approximately 6 km of road. Areas 2, 3, and 4 were essentially undeveloped at the time of the study while Area 1 consisted of forested habitats interspersed with site industrial facilities. Vegetative cover in undeveloped portions of all study areas was typical of upland portions of the SRS.

METHODS

Removals

We implemented removals between November 2001 and March 2002. The removal methods consisted of some combination of targeted roadside dog hunts and sharpshooting by project personnel. The targeted roadside dog hunts were organized similar to standard management hunts and were implemented by the deer hunt crew from Westinghouse Savannah River Company. However, these hunts were specifically designed to remove deer from the 3-km-wide road corridor around the target roadway. Hunts consisted of approximately 50 dog packs and 20 stationary standers; all dog release points and stand locations were within the 3-km corridor. Interviews with successful hunters confirmed that most kills occurred within the target corridor. Sharpshooting was conducted by project personnel primarily by spotlighting and shooting deer from vehicles during nighttime hours. The sharpshooting treatment differed from dog hunts both in the intensity of removal and in the width of the removal area. Dog hunts removed deer from the entire 3-km corridor but sharpshooting was limited to a smaller, 1-km corridor (0.5 km on each side of the target roadway).

We assigned the 4 road areas to 4 removal methods as follows: Area 1—dog hunts during both years; Area 2—dog hunts during year 1 only; Area 3—dog hunts during year 1 plus sharpshooting; and Area 4—dog hunts during year 2 only. We implemented the year 1 removals in fall 2001 and winter 2002 as described below. In Area 1, we implemented 2 targeted dog hunts (17 November 2001 and 1 December 2001). Area 2 also received 2 targeted dog hunts (8 December 2001 and 15 December 2001). Finally, we implemented 1 dog hunt on Area 3 (24 November 2001), and then conducted sharpshooting 3–5 nights per week from 27 November 2001–1 March 2002. Area 4 was not subjected to removals in year 1, so it served as an untreated, control area. Due to security concerns at the SRS, all standard management hunts were canceled for fall 2001. Therefore, the deer removed for this study were the only deer removed from SRS by management actions between December 2000 and September 2002.

Due to management concerns about the limited number of deer removed from some areas during the 2001season, management officials implemented additional targeted dog hunt removals in 2 Areas, 1 (dog hunts both years) and 4 (dog hunts year 2 only), during the fall of 2002. These year 2 treatments included 2 targeted dog hunts in Area 1 (12 October 2002 and 19 October 2002) and 1 targeted dog hunt in Area 4 (28 September 2002). No removal treatments occurred in road areas 2 and 3 during year 2. However, the standard management hunt program was reinstated for fall 2002. The sitewide program conducted 32 hunts with 1,318 deer killed between 23 October and 14 December.

Population estimation

To measure the effects of the removals on deer population density in the road corridors, we used pellet group counts, track counts, and infrared-triggered camera counts. For the purposes of this study, we needed techniques that would allow us to detect changes in the abundance and distribution of deer within the road corridors in response to the removal efforts. Although all 3of the techniques can provide population density estimates, we used them to provide indices to population density and to detect changes over time.

Pellet group counts have been used for population density estimation and trend analysis for several species of big game animals, particularly ungulates due to their high defecation rate and relatively persistent fecal pellets (Neff 1968). Because of the relatively low deer density onsite (4–6/km^2, Johns and Kilgo in press) and the rapid deterioration of pellet groups in the Southeast (Wigley and Johnson 1981), we were concerned that conventional plot or short belt transect methods would not provide sufficient data points to be a reliable index to population density. Therefore, we conducted pellet group counts along 40 1,500-m transects per road area. Transects were perpendicular to the major roadway in each study area and extended from the roadway to the outer edge of the removal area. We counted all groups of >5 fecal pellets seen and recorded the distance from the main roadway using forester's hip chains.

We conducted track counts following the methodology of Tyson (1952) on 5.6–8 km of existing woods and logging roads in each of the 4 road areas. We counted all tracks on each road section for 5 successive nights in each survey season, using a metal drag to obliterate existing tracks each evening.

For the infrared-triggered camera surveys, we used a modification of the technique described in Jacobson et al. (1997). Due to logistical concerns with the large number (*n* = 256) of bait stations needed, we placed unbaited camera stations on areas of high deer activity such as feeding areas, habitat edges, and well-used trails. To place cameras, we overlaid a grid of 64 cells onto each road area. One camera station was placed subjectively within each grid cell for a camera density of 1 per 28 ha, about 2.5 times the camera density described in Jacobson et al. (1997). We left cameras in place for 6 nights per location in each survey season.

Population estimation efforts were initiated in late summer-early fall 2001 to obtain index values prior to removal treatments. All efforts were completed in each road area before the initiation of any deer removals (i.e., hunts or sharpshooting) in that area. We then repeated the index surveys in late summer-early fall in 2002 and 2003 to obtain population indices for 2 years post-removal. For all estimation techniques, we used the same locations (transects, roads, or camera stations) in successive years.

Data analysis

In evaluating the effectiveness of the localized removals, we considered two primary objectives in the analysis of population index data. First, an effective localized management strategy should reduce deer abundance in the road corridor for 2 years following the removal. Second, we expected that our removals would affect the distribution of deer abundance within the road corridor, particularly for Area 3 (sharpshooting), where our deer removal was concentrated within a 1-km corridor around the central roadway. If deer did not alter their home ranges to occupy this vacated habitat, then we would expect the post-removal distribution of deer abundance to show lower density in this small corridor than near the periphery of the 3-km-wide corridor (McNulty et al. 1997). This effect would not be expected in the dog-hunt only treatments, where removals were distributed evenly throughout the 3-km corridor.

To examine the effects of removals on abundance, we compared the population index values in 2002 and 2003 to the pretreatment 2001 values. Depending on the normality of the index data as revealed by Shapiro-Wilkes *W* tests and examination of probability plots, we used either paired *t*-tests or nonparametric Wilcoxon signed-rank tests to determine whether the measured indices differed between years. We used sequential Bonferroni correction to account for multiple comparisons within areas (Rice 1989). Throughout the data analysis, we used the results of the 3 population indices as complementary data in a weight-of-evidence approach to assess changes over time. The use of 3 independent indices provides more confidence than a single index.

To examine potential changes in deer distribution, we used a combination of 2 statistical tests. For the pellet group counts, we tested whether the mean distance from a pellet group to the central roadway changed using single factor analysis of variance (ANOVA). If the distribution of deer density changed among years in response to the treatments, we would expect to see a change in the average distance from the road between pre- and post-removal periods. For the track and camera counts, we used repeated measures ANOVA. The camera locations were divided into 4 distance categories (0–375 m, 376–750 m, 751–1125 m, 1126–1500 m) and distance category was the main effect in the ANOVA. A significant interaction between distance and time indicated a change in distribution. The track count analysis was similar, except that we could only use 2 distance categories (0–750 m and 751–1500 m).

In addition to the statistical analyses, we used graphical analysis to examine the changes in population indices over time. To allow us to compare values from different indices on the same graph, we standardized the index data by expressing each value as a proportion of the maximum for that index in that road area, as

$$Z_{ij} = \frac{X_{ij}}{RMAX_i}$$

where Z_{ij} is the standardized value, X_{ij} is the original value, and $RMAX_{ij}$ is the maximum value for the method in the road area (Romesburg 1990). These standardized values were used only for graphical representation and not in the statistical analysis. All statistical analyses were performed in SAS (SAS Institute, Cary, NC, USA).

RESULTS

Removals

During fall 2001 and winter 2002, we removed 12–43 deer from the 3 targeted removal areas (Table 5.1). The additional efforts in fall 2002 removed 21–23 deer from 2 removal areas. Based on the 2000 deer population density of approximately 4 deer/km^2 (Johns and Kilgo in press), the total removals over the 2-year period removed between 32% and 60% of deer that occupied the 3-km-wide road corridors at the beginning of the study. Using the same density data, the sharpshooting in Area 3 removed more deer (30) than density estimates would predict in the 6 km^2 smaller corridor (24). Although no technique can remove 100% of white-tailed deer in forested habitats like the SRS, this combination of methods appeared to be highly effective in removing deer from this limited area.

Area 1 (dog hunts both years)

The roadside dog hunts in 2001 met with limited success in Area 1, as 12 deer were removed from the road corridor. For this reason, additional hunts were conducted in 2002, with better results (Table 5.1). The results of our population indices reflect these removals, with all indices showing a decline for the entire study period (Fig. 5.1). Statistically, 2001 did not differ from 2002 for track counts ($n = 7$, $t = 3.34$, $P = 0.016$), pellet counts ($n = 40$, $S = 36$, $P = 0.305$) or camera counts ($n = 64$, $S = 131.5$, $P = 0.052$) after Bonferroni correction. In contrast, 2003 differed from 2001 for pellet counts ($n = 40$, $S = 63$, $P = 0.004$) and camera counts ($n = 64$, $S = 221$, $P = 0.001$) while the track count values did not differ ($n = 7$, $t = 2.38$, $P = 0.055$). Our analyses did not indicate any change in the distribution of deer in Area 1 ($P > 0.28$ for all 3 indices).

Area 2 (dog hunts year 1 only)

We conducted 2 dog hunts in Area 2 in fall 2001 that removed 43 deer. We did not conduct removals in this area in 2002, although adjacent hunt compartments were hunted as part of the standard management program. The population indices declined sharply from 2001 to 2002 for all 3 indices, followed by stabilization or, in 2 of 3 indices, an increase in 2003 (Fig. 5.2). Statistically, 2002 differed from 2001 for all 3 indices (track counts: $n = 8$, $t = 3.29$, $P = 0.013$, camera counts: $n = 64$, $S = 155$, $P = 0.002$, pellet counts: $n = 40$, $S = 110$, $P = 0.012$). In contrast, the 2003 year also differed from 2001 only for camera counts ($n = 64$, $S = 186.5$, $P = 0.003$). The track count ($n = 8$, $t = 2.82$, $P = 0.026$) and pellet count ($n = 40$, $S = 43.5$, $P = 0.29$) data were not different from 2001 after correction for multiple tests, reflecting the increase observed in 2003 (Fig. 5.2). We observed no evidence for a change in distribution of the deer population in Area 2 ($P > 0.46$ for all 3 indices).

Area 3 (dog hunts year 1 and sharpshooting)

In the 2001 removal season, we removed the same number of deer (43) from Area 3 that we did from Area 2 (Table 5.1). However, in Area 3, 30 of the deer (70%) were removed by sharpshooting from within the smaller 1-km corridor around the road. All population indices showed a decline in 2002 compared to 2001, with 2 of 3 showing a continued decline or stabilization in 2003 (Fig. 5.3). The track counts, however, showed an increase in 2003 compared to 2002. The track count ($n = 8$, $t = 3.57$, $P = 0.0091$) and pellet count ($n = 40$, $S = 102$, $P < 0.001$) data differed significantly from 2001 to 2002 but the camera data indicated no change ($n = 64$, $S = 29$, $P = 0.65$). The same pattern held in 2003 compared to 2001, with track ($n = 8$, $t = 3.53$, $P = 0.010$) and pellet ($n = 40$, $S = 138$, $P < 0.001$) data different and no change in camera data ($n = 64$, $S = 113$, $P = 0.055$). Contrary to our expectations, we found little evidence for any changes in the distribution of deer in Area 3 ($P > 0.15$ for all three indices).

Area 4 (dog hunts year 2 only)

Area 4 was an untreated control in the 2001–2002 removal season; however, targeted dog hunts removed 23 deer in the fall of 2002 (Table 5.1). The pellet count ($n = 40$, $S = 0$, $P = 1.0$) and camera count data ($n = 64$, $S = 2.5$, $P = 0.96$), showed no change from 2001 to 2002 (Fig. 5.4). The track count data were not statistically different ($n = 7$, $t = 0.87$, $P = 0.36$), but the graph indicated a slight decline. Graphical presentation suggested a decline in all 3 indices in 2003 compared to 2001; however, the track counts ($n = 7$, $t = 2.79$, $P = 0.032$), pellet counts ($n = 40$, $S = 57.5$, $P = 0.071$) and camera counts ($n = 64$, $S = 18.5$, $P = 0.73$) did not show a statistical difference. There was no evidence for a change in distribution in Area 4 ($P > 0.16$ for all 3 indices).

DISCUSSION

Our results indicate that abundance of white-tailed deer in forested road corridors was reduced following the implementation of localized management removals in those road corridors, at least in the short term. In years following removal of >33% of the estimated population in the 18-km^2 removal areas, including 2002 for Areas 2 and 3 and 2003 for Area 1, 7 of 9 (78%) of our population index measurements suggested a significant decline in deer abundance within that corridor. This is especially noteworthy considering that the standard management hunts did not occur in 2001, so that the sitewide population was presumably increasing during the period from fall 2000 to fall 2002. The results of population indices in the untreated Area 4 support the idea that a sitewide population decline does not explain our observations in the remaining road areas.

Our results suggest that localized management reduced population density for 1 year in a limited area while population density in surrounding areas was unaffected. However, the real value of the localized management concept lies in the persistence of the low density area over time (Porter et al. 1991). McNulty et al. (1997) found that reduced population density persisted in their 1.4-km^2 removal area for 2 years after the removal action. Our results in relation to this assessment were less clear, as only 3 of 6 (50%) population indices were significantly reduced 2 years after the removal compared to 78% after 1 year. An upward trend was evident in some indices 2 years after the removals (see Figs. 5.2, 5.3). Unfortunately, management concerns required additional removals in 2 areas in the second year of our study so we could not evaluate the persistence of reduced density in Area 1.

We did not observe evidence that the distribution of deer abundance within the road corridors changed in response to the management treatments. We expected to see a change in Area 3, where sharpshooting was limited to a small, 1-km-wide corridor. This 6-km^2 corridor is more than 4 times larger than the 1.4-km^2 successful removal area in McNulty et al. (1997). We observed a slight trend for the mean distance to pellet groups to increase over time, but the change was not significant and the other indices did not suggest any change in distribution. The overall low population density at SRS and our lack of spatial replication of this removal method may have limited our ability to detect distribution changes statistically.

Several lines of evidence suggest that localized management may not function at the SRS as effectively as Oyer and Porter (2004) observed in New York. Our observation of little effect on distribution in Area 3 indicated that the concept may not be effective for small areas (< 10 km^2) at SRS. Mean home range sizes for adult does at SRS were similar to those observed in the Adirondacks (197 ha [Comer et al.2005] versus 221 ha [Tierson et al. 1985]), so differences in home range size did not explain this difference. Our data also indicated that the reduced population density may not persist for the 5-year period found by Oyer and Porter (2004). Although population indices indicated reduced abundance 2 years after the removals, 3 of 6 indices suggested increasing trends in 2003 compared to 2002 in road areas that were not treated in the 2002 removal season (see Figs. 5.2 and 5.3). Management hunts resumed in the 2002–2003 season, so the sitewide deer population was probably decreasing or stable for that period.

Social and genetic structure in white-tailed deer at SRS provides a potential explanation for the observed differences in the efficacy of localized management. The localized management concept as outlined by Porter et al. (1991) is based on assumptions regarding the existence of tightly bound, matrilineal social groups among female deer, resulting in low female dispersal and high philopatry. Mathews and Porter (1993) found 8 genetically distinct matrilineal social groups in the Adirondack study area and the localized management test by McNulty et al. (1997) involved the removal of one of these groups. Using microsatellite genetic data and radiotelemetry, Comer et al. (in press) found that closely related female deer at SRS did not form persistent, cohesive social groups and found evidence for high (>20%) dispersal rates among young does. In a concurrent study, Comer (2004) found that deer from the removal areas described herein did not form genetically distinct groups as Mathews and Porter (1993) describe. Despite these observations, population density in the road corridors was reduced 2 years after the initial removals, suggesting that the success of the concept may not be strictly tied to the underlying population model. However, the lack of cohesive sociogenetic structure in the population may explain why the smaller removal area was not effective. In combination with elevated female dispersal, it also explains why the population reduction may not persist over longer time periods.

MANAGEMENT IMPLICATIONS

This study represents an important field test of the localized management concept for white-tailed deer management. Due to its potential economic and social benefits for deer managers, this concept has been widely proposed as a solution to overabundant deer problems in forested (Campbell et al. 2004, Oyer and Porter 2004) and urban/suburban (Kilpatrick and Spohr 2000, Grund et al. 2000, Porter et al. 2004) landscapes. However, field tests of the concept are limited to a single removal experiment conducted by the researchers that first described the concept. The experiment described by McNulty et al. (1997) and Oyer and Porter (2004) provided an important pilot test of the feasibility of the concept. However, the deer population at the Adirondack Mountain study site is a low density, unexploited herd that undergoes seasonal migrations associated with severe winter conditions. The old age structure, limited competition for space, and seasonal migration all contribute to the development of strong social structure, creating an ideal situation for the localized management concept (Mathews and Porter 1993, Nelson 1998). These conditions, however, may not represent those encountered by deer managers in every situation. Furthermore, the deer removed by McNulty et al. (1997) were selected based on detailed knowledge about social affiliations that would not be available to most deer managers. More likely, managers will identify an area of concern geographically and conduct the removal in that area; similar to the removals we conducted.

Despite the differences between our study and the previous test of localized management, we found that our techniques were potentially effective for removal of deer from a localized area for a 1–2 year period. Our data suggest that targeted management hunts utilizing the services of local hunters were as effective as a more intensive program utilizing spotlighting and sharpshooting. Based on the results of our test of the localized management concept, as well as data regarding social and genetic structure in deer at SRS, caution should be exercised when applying the localized management concept to small removal areas like the one described by Oyer and Porter (2004). The behavioral and social plasticity of white-tailed deer has been well-documented (e.g., Marchinton and Atkeson 1985, Miller and Ozoga 1997), and should be kept in mind when advocating any management strategy based on deer sociobiology.

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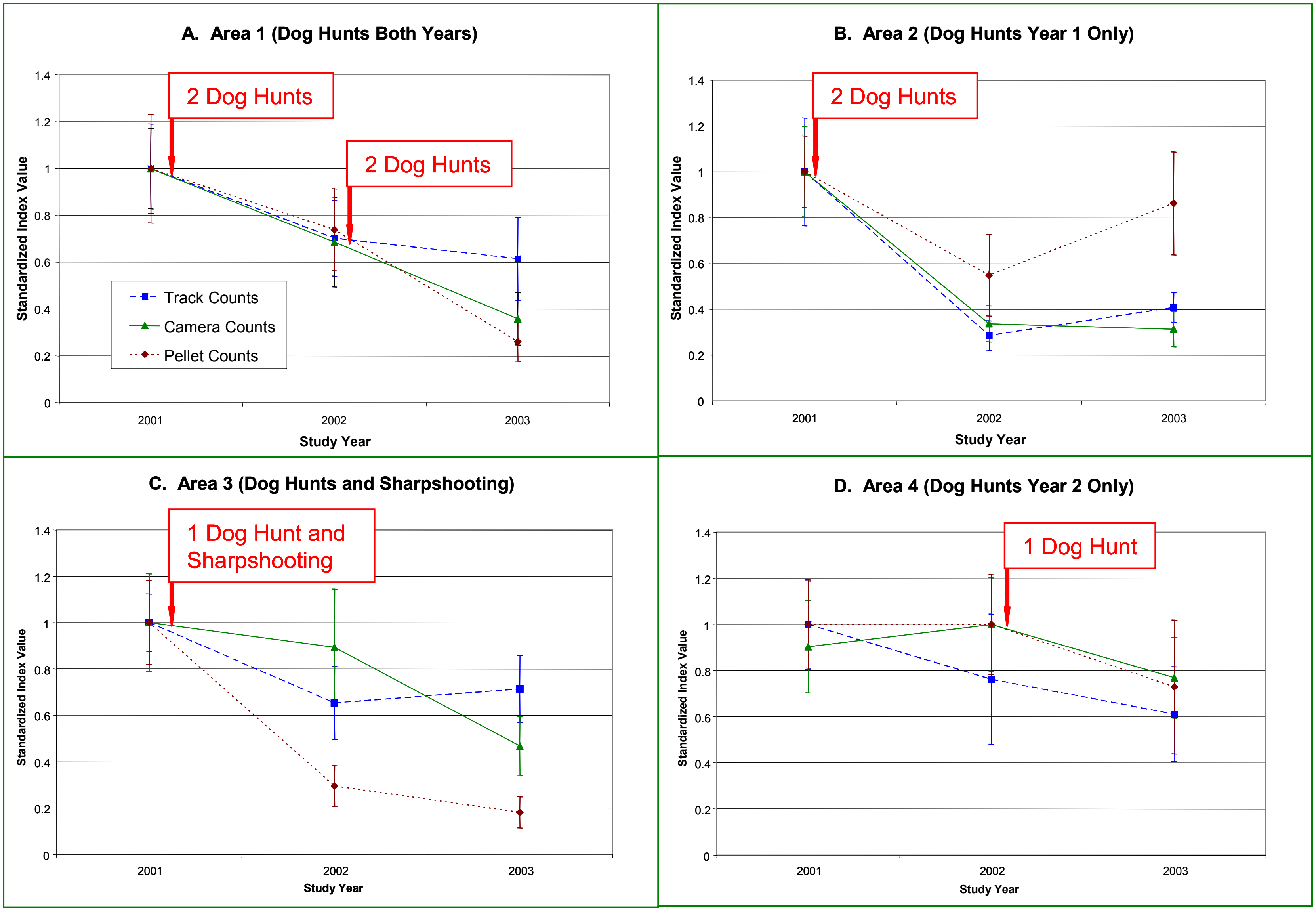
Table 5.1. Numbers of male and female white-tailed deer killed in experimental removals by removal method at 4 road areas on the Savannah River Site, Aiken, South Carolina in 2001 and 2002.

		Number Removed		
Road Area	Removal Method	Males	Females	Total
1 (Dog hunts both years)	2001 Dog Hunts	7	5	12
	2002 Dog Hunts	12	9	21
2 (Dog hunts Yr 1)	2001 Dog Hunts	17	26	43
3 (Dog hunt + Sharpshooting)	2001 Dog Hunt	7	6	13
	Sharpshooting	9	21	30
4 (Dog hunt Yr 2)	2002 Dog Hunt	14	9	23

Figure 5.1. Results of population index measurements before and after white-tailed deer removals in 4 removal areas at the Savannah River Site, Aiken, South Carolina, in 2001–2003. Index values are standardized to allow comparisons and error bars indicate standard error of index measurements.


A. Area 1 (Dog Hunts Both Years)
2 Dog Hunts
2 Dog Hunts
Track Counts
Camera Counts
Pellet Counts
Standardized Index Value
Study Year
1.4
1.2
1
0.8
0.6
0.4
0.2
0
2001
2002
2003
B. Area 2 (Dog Hunts Year 1 Only)
2 Dog Hunts
Standardized Index Value
Study Year
2001
2002
2003
C. Area 3 (Dog Hunts and Sharpshooting)
1 Dog Hunt and Sharpshooting
Standardized Index Value
Study Year
2001
2002
2003
D. Area 4 (Dog Hunts Year 2 Only)
1 Dog Hunt
Standardized Index Value
Study Year
2001
2002
2003

CHAPTER 6

CONCLUSIONS

The results of my analysis call into question the universal applicability of currently proposed models of white-tailed deer population structure and management. In particular, the rose-petal model of population expansion was developed to describe female population expansion and structuring in the Adirondack Mountains of New York (Porter et al. 1991). However, attempts have been made to generalize the rose-petal model and the localized management concept that relies on it to other portions of the species' range (e.g., Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004). The results of my study emphasize the plasticity of white-tailed deer social behavior noted by other authors (Marchinton and Atkeson 1985) and suggest that the usefulness of the localized management concept will vary depending on characteristics of local deer populations. The localized management concept may still be a useful tool for deer managers; however, they should acquire data on range fidelity, dispersal, and family group structure to accurately predict the results of a localized management program.

My analyses of the SRS deer population suggest that it exhibits different spatial and genetic structure than the Adirondack population. Female deer in the Adirondack population formed persistent, matriarchal social groups that represented genetically distinct units (Mathews and Porter 1993). Females exhibited a high degree of philopatry with closely related individuals occupying overlapping home ranges. I found that female kin groups were considerably less persistent at SRS and that related individuals often were spatially quite distant. In contrast to previous work showing genetic structure in white-tailed deer populations (e.g., Purdue et al. 2000, DeYoung et al. 2003), I found that the entire 800-km^2 SRS was a single, panmictic genetic unit. Although I collected limited direct evidence of female dispersal, genetic evidence suggested that female dispersal may be elevated and that female dispersal rate was not significantly less than male dispersal rate.

My analysis of removal actions along road corridors at SRS generally agreed with these results. In a previous test of localized management, the removal deer consisted of closely related females from a 1.4-km^2 area (McNulty et al. 1997). In that population, social groups like the removal deer formed genetically distinct units (Mathews and Porter 1993). In contrast, I found that deer removed from 18-km^2 corridors adjacent to major roadways at SRS did not represent genetically distinct units when compared to surrounding background habitats. However, population indices suggested that the removals resulted in short-term reductions in population density in the road corridors. It may be that the localized management concept is not strictly dependent on deer following the rose-petal hypothesis for population expansion. Index data from 2 years post-removal indicate that reductions may not persist over the long term and population distribution data suggest that the concept did not operate at the small spatial scale observed in the Adirondacks (McNulty et al. 1997).

The management history of the SRS population provides a logical explanation for the contrast between my results and those observed in the Adirondack population. The SRS population has been intensively managed for nearly 40 years, with annual harvests between 20% and 37% of the estimated prehunt population size between 1990 and 2000. The harvest is nonselective for gender and age, and has resulted in a young age structure among does. In 2002, 71% of does killed were <3 years old and less than 4% were in age classes >5.5 years. The greatest degree of spatial structure in the Adirondack population was observed in older (> 5 years) does (Aycrigg and Porter 1997). At SRS, the lack of older matriarchal females may prevent the formation of cohesive, persistent social groups. Orphaned female fawns tend to disperse more often than non-orphaned fawns, so the harvest may contribute to greater dispersal of young does as well (Etter et al. 1995). The plasticity of white-tailed deer social behavior in response to differing geographic area and habitat is well established (Miller et al. 2003). My results suggest that management history also can cause variation in social behavior and population structure.

LOCALIZED MANAGEMENT AT SRS

Although the localized management concept may hold some promise for addressing deer-vehicle collision concerns at SRS, my results suggest that a management program relying on this concept should be monitored to determine its long-term effectiveness. My examination of population spatial and genetic structure suggests that the white-tailed deer population at SRS does not behave according to the rose-petal model of population expansion. Of particular concern for the localized management concept, genetic analyses at both local and landscape scales indicated elevated dispersal of female deer between putative subpopulations. Low female dispersal is one of the fundamental assumptions of the rose-petal model (Porter et al. 2004). If colonization of vacant habitats by female deer occurs frequently, that would reduce the time period that population density reductions persist following localized removal.

Although the results of this study suggest that the rose-petal model does not apply to the SRS deer population, the results regarding the potential effectiveness of localized management are less certain. Localized management may not be strictly tied to the rose-petal model. Population index data from SRS indicate that the removal actions successfully reduced population density in the 3-km road corridor for 1–2 years following removals. For management purposes, the targeted roadside dog hunts were as effective as sharpshooting in reducing population density in the road corridors. The former is a more viable alternative for site management due to its use of private hunters to remove deer while providing recreational opportunities.

Although I found that removals in the road corridors successfully reduced population density in the short term, the implications for deer-vehicle collision rates are not clear. The number of deer-vehicle collisions is dependent on many factors, the most important of which is traffic volume (Novak et al. 1999). In fact, historic data show that SRS workforce size predicted the number of deer-vehicle collisions as effectively as prehunt deer population (Novak et al. 1999). For this study, SRS workforce allocations led to drastic traffic flow changes on the roads through the 2 most intensive removal areas. Thus, the numbers of deer-vehicle collisions on these road sections was uniformly low (<5 per year) during the study (both before and after removals) compared to previous years. The number of deer-vehicle collisions on these 2 road sections declined from pre-removal (9 in 2000, 7 in 2001) to post-removal (4 in 2002); however, the low totals make these data difficult to interpret. The sitewide number of deer-vehicle collisions essentially remained unchanged (92 in 2001, 87 in 2002) during the removal period.

For future management related to deer-vehicle collisions, I would recommend a program of targeted dog hunts in the roadside corridors similar to those implemented in this study. These hunts should be conducted along road stretches with historic deer-vehicle collision problems and/or high traffic volume. Because of concerns about the persistence of population density reductions, each road section should be hunted at intervals of 2-5 years, and population monitoring should be conducted in road sections subject to targeted hunts. A program of this type has the potential to maintain reduced deer population density in the road corridors and, hopefully, reduce the number of deer-vehicle collisions on target road sections.

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