SOCIOSPATIAL CHARACTERISTICS AND GENETIC STRUCTURE OF WHITE-TAILED DEER IN THE CENTRAL APPALACHIANS OF WEST VIRGINIA

by

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(Under the Direction of Karl V. Miller)

ABSTRACT

Despite numerous investigations of deer sociobiology and genetic attributes, the effects of social organization on the genetic structure of white-tailed deer (*Odocoileus virginianus*) populations are not well understood. Furthermore, previous investigations of deer sociobiology have typically focused on low-density and/or migratory populations. Given the considerable behavioral plasticity documented in white-tailed deer in different demographic contexts, sociobiological attributes among populations will vary accordingly. I compared sociospatial characteristics and genetic structure of female white-tailed deer (*Odocoileus virginianus*) inhabiting a forested environment in the central Appalachian Mountains. I utilized an extensive telemetry dataset for 127 female white-tailed deer captured during the winters of 1999-2002 on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) in West Virginia. I delineated spatial groups of female white-tailed deer and used genetic measures to evaluate spatial and genetic relationships. I also evaluated a genetic marker panel in the context of a group of closely related individuals, and used this genetic information to retrospectively assess the relatedness of both the deer included in an experimental removal and those remaining. My results demonstrate that female white-tailed deer do not distribute themselves randomly across the landscape of my study area, but are clumped into groups of spatially tolerant individuals. My

data also suggest that while the patterns of inter-relatedness observed in our study are consistent with matriarchal social structure reported in previous studies, higher population density may affect the composition of deer groups removed in spatially-based localized management efforts. Overall, the rose-petal model of white-tailed deer population expansion applies to my study population, but high population density forces overlap among matriarchal groups and may limit the effectiveness of localized management efforts.

INDEX WORDS: Central Appalachians, Genetic structure, Home range overlap, *Odocoileus virginianus*, Matrilineal group, Social group, Sociospatial, White-tailed deer

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DEDICATION

I dedicate this dissertation to my wife, Stephanie, and my parents, John and Suzanne. I am forever indebted to my parents, who have never ceased to provide moral support for all of my pursuits. I thank you for your encouragement of my academic career, and for your unconditional generosity throughout the years. My wife has brought me more happiness than I can express and has displayed formidable patience, encouragement, and understanding as she helped me attain this goal.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

White-tailed deer (*Odocoileus virginianus*) are among the most widespread and intensively-studied North American big game species. The many habitats and physiographic regions successfully inhabited by white-tailed deer are testament to the species' adaptability and tremendous behavioral plasticity (Hirth 1977). While information on population attributes is routinely collected, behavioral data are often much more difficult to obtain (Miller and Ozoga 1997). Until recently, female social structure was oversimplified, and continues to be misunderstood with respect to population parameters and geographic variation (Ozoga et al. 1982, Ozoga and Verme 1984, Mathews and Porter 1993, Miller and Ozoga 1997).

Because female social structure affects the spatial arrangement of home ranges, it is especially of interest in the management of white-tailed deer impacts on a landscape. Though studies over the past two decades have shed considerable light on the role of sociobiology on spatial structure of female whitetails, the selective pressures responsible for this social structure are poorly understood (Mathews 1989). As a result, neither the selective pressures nor the adaptive values associated with social structure have been established. Furthermore, the effect of this sociospatial structure on underlying genetic structure has been limited by biologists' abilities to measure genetic variation on a sufficiently fine scale (Mathews et al. 1997).

Much of the previous research of female social structure was based on study of captive, unhunted, and/or migratory populations. Although these studies were instrumental in establishing some sociobiological parameters of female white-tailed deer, it is not known to what extent these

observations are applicable to populations across the species' range. More recently, an alternate deer management strategy has been formulated, and if applicable could alleviate conflicts associated with overabundant white-tailed deer in a variety of contexts.

Without knowledge of the underlying female social structure of a population, attempts to apply new management strategies may fail for unknown reasons. It is necessary to test new management strategies in a variety of contexts before accepting that these methods are universally applicable (Miller 1997, Miller and Ozoga 1997). It is also necessary to determine what sociobiological factors ultimately determine the technique's success or failure. Furthermore, recent technical developments allow measurement of genetic attributes of populations, social groups, and individuals at a resolution not available in previous studies of white-tailed deer social structure. Together with describing genetic attributes at a microscale, new genetic techniques also can provide insight into potential population genetic effects of new management strategies. With the aforementioned points in mind, the present study investigates the sociobiological attributes and underlying genetic structure within a population of white-tailed deer in the central Appalachians of West Virginia. This study originated due to the need to evaluate the applicability of an alternate management strategy in an area where overabundant white-tailed deer detrimentally alter forested ecosystem processes.

Literature Review

Female social structure

The fundamental social organization of white-tailed deer was traditionally considered a simple dominance hierarchy, where dominance is directly related to age (Hirth 1977), and social status largely dictates individual behavior (Marchinton and Hirth 1984). Marchinton and Atkeson's (1985) application of the concept of facultative territoriality recognized the

importance of spatial considerations on white-tailed deer sociobiology. The social structure and spatial relationships exhibited by female white-tailed deer have been attributed to matrilineal kinship (Aycrigg and Porter 1997, Hawkins and Klimstra 1970, Hirth 1977, Mathews and Porter 1993, Nelson and Mech 1981, Nixon et al. 1991, Ozoga et al. 1982). Particularly, female social structure is considered to be a matriarchal group composed of three to four generations of females and their offspring (Hawkins and Klimstra 1970, Mathews and Porter 1993). Early observations of female white-tailed deer sociobiology noted similar home ranges of a doe and her fawns and suggested that preference for that range might be transferred across generations. Young fawns tend to have very small ranges, but as they mature their ranges approximate that of their mother. Additional observations included numerous examples of similarity in offspring/parent home range affinity, including some spanning three generations (Marchinton and Hirth 1984).

While early studies established the generalized female social structure, a series of studies conducted within an 252-ha enclosure at the Cusino Wildlife Research Station in Michigan investigated the relationship of demographics, deer biology, and sociobiology (Ozoga et al. 1982, Ozoga and Verme 1984). Specifically, these studies provided insights into the spatial arrangement of home ranges within female social groups, especially in the context of the fawning period. Alhough white-tailed deer have not generally been considered territorial (Smith 1976, Coblentz 1977), Ozoga et al. (1982) observed that pre- and post-parturitient females isolated themselves from others and exhibited territorial characteristics for approximately 4 weeks. Within family groups, matriarch does ($\geq$ 4 years old) occupied and defended the same fawning area year after year, whereas 3-year-olds established fawning areas away from the family group. Yearling and 2-year-old does occupied areas adjacent to, but exclusive of the

matriarch's fawning area. At high population densities, this territoriality caused marked reductions in neonatal survival rates for 2- and 3-year-old mothers. Apparently, maternal domination effectively suppressed productivity of 3-year-old females who were still associated with their matriarchal group. While Ozoga et al. (1982) observed that females typically isolated themselves from other adults for 2 weeks before and 4 weeks after parturition, more recent research suggests this pattern of maternal segregation may persist longer than previously thought. Bertrand et al. (1996) found that reduced sociality of radio-collared does may persist at least 18 weeks after parturition at moderate population densities.

Adaptive value of female social structure

Limited evidence exists regarding the adaptive value of social structure in white-tailed deer. Social groups of white-tailed deer in forested habitats tend to be smaller than those in open habitats (Hirth 1977). Jarman and Jarman (1979) observed similar patterns in species of African antelopes relative to habitat, predation, and social structure. Messier and Barrette (1985) found that winter "yarding" behavior of northern white-tailed deer provided more effective escape from predation attempts. A series of studies in the Adirondack mountains of New York spanning almost 30 years considered possible anti-predatory functions of home range location within female social groups (Mathews 1989). This study predicted that dominant does (matriarchs) would occupy the most preferred position within a social group's home range, and that the matriarch's youngest daughters would be allowed to share this home range, exclusive of the matriarch's older daughters. Home ranges of young does (<2 years old) almost completely overlapped the home ranges of older deer. This observation was explained, in part, as an anti-predator tactic. Also, significant home range overlap among all individuals within a social group suggested that white-tailed deer in forested environments were more social than previously

thought. Mathews' (1989) results supported the hypothesis that individual home ranges are not randomly located within social groups. Nonetheless, direct evidence of kinship of social group members was lacking in this and other studies.

High home range overlap between mother and young also may reduce the amount of intraspecific aggression the young must tolerate, as has been suggested in red deer (*Cervus elaphus*, Clutton-Brock et al. 1982). Furthermore, Clutton-Brock et al. (1982) reported that within groups of red deer, young were generally located within 10m of their dams, and that barren mothers remained closely associated with their previous year's offspring. The frequency of mother-daughter association was inversely proportional to the age of the daughter. If applicable to white-tailed deer, high levels of home range overlap between a mother and her young (< 2 years old) might insulate offspring from unnecessary intraspecific aggression. When a female daughter begins to bear offspring and compete with her for resources, a matriarch forcing her 3-year-old daughter(s) to a peripheral position would be advantageous for both. Maternal investment theory (Trivers 1974) predicts that mothers should care for their young until the mother's future reproductive potential is threatened. Mothers would be expected to decrease their input when the offspring becomes reproductively mature and the mother's resources are better spent on the production of more young of her own.

In a New York study, Aycrigg and Porter (1997) considered groups of white-tailed deer to be relatively stable through time (with respect to membership), while variation in sociospatial behavior at the individual level was related to age and reproductive status. Stability of matrilineal groups over time may be due to the benefits derived from the presence of additional females in the vicinity. Additionally, familiarity with a geographical area may enhance reproductive success. If older females have access to, and familiarity with local resources,

younger female offspring will likely benefit from remaining close to their mother (DeGayner and Jordan 1987). Aycrigg and Porter (1997) observed that among deer >5 years old, females maintained relatively distinct home ranges from other individuals of the same age class. Older females were clustered with younger females more often than with other older females. Mathews (1989) reported similar results when home ranges were plotted sequentially by age within matrilineal groups. Aycrigg and Porter (1997) suggest that the lack of a detectable spatial pattern in home ranges of ≤5 year old deer means that younger, subordinate females may be unable to maintain exclusive home ranges. Younger females may receive benefits, (high quality habitat, anti-predator functions, knowledge of migration routes) by sharing ranges with older, dominant females. Similarly, Nelson and Mech (1984) suggest that younger females do not establish their own matriarchal groups with their own female offspring until they are >5 years old. Aycrigg and Porter (1997) concluded that the exclusive ranges of older females in their study may have reflected social dominance. Even though no independent measure of dominance was available, this is consistent with observations of other species where age and dominance are directly related (Franklin and Leib 1979, Clutton-Brock et al. 1982).

Because of an almost complete lack of hunting on the New York study area, Mathews (1989) concluded that an older age structure aided in social group formation and stability that resulted from very high levels of female philopatry. Further, based on high philopatry and matriarchal dominance structure, they predicted that individual home ranges within each social group would approximate petals of a rose, where the matriarch was located in the middle with younger group members (daughters) forming adjacent and overlapping home ranges radiating away from the matriarch's. These observations and predictions were subsequently used to

formulate the rose-petal hypothesis, a behavior-based model of white-tailed deer population expansion (Mathews 1989, Porter et al. 1991).

Applied sociobiology: Localized management

Until recently, deer sociobiology has rarely been incorporated into strategies of population management. The "rose-petal hypothesis" formulated by Mathews (1989) was the first to utilize information on female social structure to more efficiently focus management efforts based on sociobiological principles. The New York researchers proposed that removal of one or more matriarchal social units could serve as an alternate management strategy to be used in overabundant populations. This technique would potentially allow managers to alleviate detrimental effects associated with overabundant white-tailed deer on a local scale, thereby being more practical in many contexts than widespread population reduction. Following the removal of a social group of female deer, the philopatry of adjacent groups should theoretically prevent rapid recolonization. Thus, a persistent localized zone of low deer density could persist for 10-15 years (Porter et al. 1991). This localized management concept was tested to a limited extent by McNulty et al. (1997), based on the same social groups delineated by previous researchers in the Adirondacks. A group of 14 does were removed, and 9 radiocollared females belonging to adjacent social groups were monitored. A localized reduction in deer density was achieved.

The rose-petal hypothesis was based on the study of an unhunted population in which female age structure was relatively old, and is thought to resemble demographics of pre-settlement populations in that area (Mathews and Porter 1993). Due to high winter mortality of fawns, the population was relatively stable and maintained at low densities. Human-deer conflicts were not apparent, and deer were not considered "overabundant" in the Adirondack study site. Miller and Ozoga (1997) caution that significant behavioral plasticity with regard to

habitat and population demographics may limit the widespread application of behavior-based management strategies. Similarly, conclusions based on the study of one population may not always be applicable to others; in this case, the study population in the Adirondacks may not be representative of that encountered in much of the eastern United States.

Multifamily groups as demes

Geographic subdivision in mammalian genetic variation is considered the norm, and usually is the result of geographic or ecological barriers to gene flow, often resulting in the formation of geographic races distributed across a species' range (Mathews et al. 1997). The degree to which gene flow between populations is limited often determines the level of genetic diversity within populations, as well as the genetic divergence between populations. Though ecological and geographic barriers have long been known to limit gene flow, the effects of mammalian social organization on gene flow have only been explored during the past three decades (Selander 1970, Olivier et al. 1981, Chesser 1983, Melnick 1987).

Female white-tailed deer exhibit a social structure best described as matriarchal. In white-tailed deer, matriarchal social groups typically include a matriarch doe, a few generations of her daughters, and fawns (both daughters and granddaughters). All of these group members are thought to share parts of the ancestral range. Male fawns typically leave these social groups within their first or second year of life, while female fawns usually remain. Dominance within these groups is directly related to age and the matriarch of a given group traditionally occupies the best habitat and exhibits the highest reproductive success. Among sub-dominant females, rank may also be a function of the relative dominance of that individual's mother (Miller et al. 1995).

Much of the early white-tailed deer population genetics work utilized protein electrophoresis, where different forms of functionally identical enzymes (allozymes) provided information regarding the genetic diversity of various wildlife populations. Interestingly, all of the wild mammalian species with high levels of heterozygosity have large ranges and occupy a wide variety of habitats (Nevo 1978). White-tailed deer may owe their level of adaptive success in North America to this high level of genetic variability, although this speculation has not been proven (Smith et al. 1984).

Physical and biochemical evidence suggests that white-tailed deer populations are genetically subdivided into demes across short distances (Rees 1969, Harris et al. 1973, Manlove et al. 1976, Ramsey et al. 1979). In northern regions where deer migrate between winter and summer ranges, Nelson and Mech (1987) suggested that deer from separate winter yards represented subpopulations that constituted genetic demes. Adult deer from each yard occupied summer ranges exclusive of deer from neighboring yards. These relationships were predicted to persist as adult movement patterns were traditional. Most yearling females established home ranges on or near their birth ranges and continued the migration pattern of their mothers. This tendency was further expected to lead to breeding between fathers and daughters as the same dominant bucks were expected to maintain breeding tenure on their ranges for >1 year. Female philopatry was also suggested to lead to inbreeding with brothers and other close kin in instances where males never dispersed from their natal ranges. Nelson and Mech's (1987) observations were based on four deeryards separated by a minimum of 10 km in an area where deer densities were estimated between 0.2 and 0.4 deer/km^2. Deme overlap and interdeme dispersal were also observed in other areas (Nelson and Mech 1987). Strong philopatric tendencies are the most

likely influence on both individual and group home ranges (Nelson and Mech 1981, 1984, 1987) and deme characteristics are a product of this passive but significant influence.

Nelson and Mech's (1987) hypothesis of deer populations consisting of conglomerates of demes may not be limited to very sparsely populated areas with migratory deer herds. No genetic data were available to assess the level of genetic structure associated with their hypothesized demes. However, data from other deer populations and other species support the notion. Significant differences in gene frequency were found between upland and lowland deer in South Carolina (Manlove et al. 1976, Ramsey et al. 1979, Chesser et al. 1982b), among moose populations (*Alces alces*, Chesser et al. 1982a), and subgroups of other large mammals including red deer (McDougall and Lowe 1968, Gyllensten et al. 1980), reindeer (*Rangifer tarandus*, Braend 1964), and elephant (*Loxodonta africana*, Osterhoff et al. 1974).

Distinct genetic associations on a 72,000 ha area at the Savannah River Site, South Carolina, were demonstrated by Manlove et al. (1976). They suggested that genetic demes were closely associated with habitat type. In drastically different physiographic regions, both Cothran et al. (1983) in South Carolina, and Nelson and Mech (1987) in northern Minnesota suggested that white-tailed deer populations might largely be composed of inbred groups of deer as the result of consanguineous matings within matrilineally related female groups. Nelson and Mech (1987) hypothesized that wintering yards were the focal points of demes, based on habitat use, but were not able to test the hypothesis genetically. Sheffield et al. (1985) investigated genetic variation in white-tailed deer at a larger geographic scale in western Maryland, suggesting that effective population size might have been reduced due to sex-biased dispersal, harvest pressure, and dominance hierarchies. In Tennessee, Kennedy et al. (1987) found that genetic subdivisions probably existed at the sub-county level and were affected by harvest regime.

White-tailed deer are an excellent species for studies of micro- and macrogeographic genetic variation (Mathews et al. 1997). Modern theory predicts that social organization affects patterns of genetic variation within and between social groups, however markers suitable for these analyses have not been available until recently (Anderson et al. 2002, DeYoung et al. 2003). To investigate patterns of genetic variation at the level of the social group and its constituent individuals, genetic markers with high levels of genetic polymorphism on a microgeographic scale are required.

Mathews (1989) and Mathews and Porter (1993) investigated the relationships between social structure, genetic structure, and geographic location among social groups of white-tailed deer in the Adirondack Mountains of New York. They tested the hypothesis that social structure had produced genetic structure, evidenced by a greater amount of genetic variability among groups than within groups, based on highly philopatric tendencies of these matriarchal social groups. Mathews and Porter (1993) emphasized the importance of correct social group designation and concede that the resolution needed to discern among social groups on summer range (given high degree of overlap there) was ultimately higher than they were able to achieve. Another factor discussed by Mathews et al. (1997) that may have confounded analysis of genetic similarity versus spatial proximity of social groups may have been related to past fissioning of groups along matrilines. Over a period of time, older, but subdominant females may leave social groups to become the matriarch of their own group as has been documented in red deer (Clutton-Brock 1989) and in rhesus monkeys (*Macacca mulatta*, Chepko-Sade and Sade 1979). If the founding member of these new groups disperses farther than less related existing groups, spatial proximity will no longer reflect genetic similarity among social groups within a given

population. Nevertheless, the results presented by Mathews and Porter (1993) are suggestive of the role of social structure in shaping genetic structure of white-tailed deer populations.

Lack of significant shift in heterozygosity between groups observed by Mathews (1989) suggested that gene flow between social groups on her study site must have been relatively high. Twelve percent of the genetic diversity in her study was accounted for by social groups. Although this was significant, Mathews (1989) suggests that breeding males mated with females in many different groups. She concluded that male movements among social groups confounded genetic differentiation of groups of related females. Additionally, her results suggest that female philopatry had the greater influence on genetic characteristics.

Aycrigg and Porter (1997) observed that deer within one kin group had summer ranges that overlapped with several deer in another kin group, while the two groups consistently used different winter yards. This observation confirms that adjacent kin groups may overlap one another, yet still maintain group fidelity. Aycrigg and Porter (1997) also reported that once established, summer range and winter yard use appeared to be permanent, suggesting that philopatry to both can persist for long periods. Nelson and Mech (1987) reported similar observations.

The near extirpation of deer in West Virginia and much of the rest of the eastern US during the late 1800's might be predicted to result in relatively little genetic diversity in certain populations. Alternately, high levels of heterozygosity in white-tailed deer in some regions may be due to restocking efforts of the early 1900's (Marchinton et al. 1995), or due to male dispersal patterns and genetically representative breeding stock that prevented genetic drift. In more northern regions, deer populations still undergo localized population fluctuations as a result of severe winters, suggesting genetic diversity might experience periodic bottlenecks even today.

Mathews (1989) found that (contrary to their prediction) genetic characteristics on their study site were similar to those reported in deer populations throughout the eastern US (Sheffield et al. 1985, Kennedy 1987, Breshears 1988).

Genetic marker considerations

Microsatellites are short segments of DNA that contain simple repeats; the length of the repeat is usually correlated with the degree of polymorphism of that particular region (locus) of DNA. This relatively new class of highly polymorphic markers was described in 1989 (Litt and Luty 1989). Microsatellites with more than 10 dinucleotide repeats are usually considered highly informative (Weber 1990). Microsatellites are distributed randomly throughout the genome and exhibit extensive length polymorphisms (Stallings et al. 1991). The high level of polymorphism of most microsatellites makes these markers ideal for genetic analyses of wild populations of white-tailed deer (DeWoody et al. 1995) as the most conservative probability of any two individual deer having the same genotype is on the order of 2.6×10^{-8}.

Highly variable molecular markers, are especially useful for genetic studies of wildlife populations, particularly those studies focusing on establishment of parentage, evaluation of mating systems, gene flow, dispersal, and social and geographic structuring, population history, genetic bottlenecks, and hybridization (Beaumont and Bruford 1999). The widespread development and characterization of microsatellite markers, together with recent advances in automated genetic analysis provide the potential for large-scale genetic examination of wildlife populations (Honeycutt 2000). Microsatellites have allowed investigators to determine parentage of individuals in free-ranging populations, which is useful in studies of reproductive success, mating systems, and mating strategies (DeYoung et al. 2003). Recent studies using microsatellites in other large mammals have revealed unexpected mating patterns (Craighead et

al. 1995, Ambs et al. 1999, Coltman et al. 1999). Additionally, experimental and simulation data have supported the statistical reliability of these methods in wild populations (Slate et al. 2000).

A panel of microsatellite loci developed for use in genetic studies of white-tailed deer was developed by Anderson et al. (2002). DeYoung et al. (2003) evaluated a subset of these markers to gauge their general performance in diverse populations of white-tailed deer. They confirmed that these markers are highly accurate for parentage assignment in both pedigreed captive and free-ranging deer. Thirteen free-ranging white-tailed deer populations spanning 3 subspecies were sampled to assess possible geographic limitations of the panel. Several loci in each population deviated from Hardy Weinberg equilibrium, but removal of these loci did not decrease overall exclusion probabilities for any population below 0.99 and had minimal effect on other population statistics. Population statistics, including alleleic diversity, heterozygosity, exclusion probability, and others were similar among free-ranging populations, while statistics for one captive population detected probable genetic substructuring. They predict that this panel of microsatellite loci will be applicable and informative in most white-tailed deer populations. A large number of loci, high allelic diversity, and absence of linkage add to the usefulness of the panel. Finally, the resolution of the panel is deemed sufficient for studies of parentage exclusion and population assignment based on genotypes (DeYoung et al. 2003).

Study objectives

The goal of my research is to enhance our understanding of the sociospatial structure and underlying genetic structure of nonmigratory populations of white-tailed deer. The most immediate application is an evaluation of the rose-petal hypothesis and the associated concept of localized management of overabundant populations. White-tailed deer social interactions are often oversimplified, but are known to be quite plastic with regard to geographic area, habitat,

and population parameters. It is not the intent of this work to provide a model with which the social framework of populations across the species range may be exactly predicted. It is, however, realistic that this work will be helpful in describing social structure of a nonmigratory herd, contrasting it with previous observations from migratory herds, and drawing conclusions helpful both to students of mammalian social structure and wildlife biologists charged with managing growing white-tailed deer populations on a landscape increasingly dominated by human activity.

The five chapters address the goal of this research from differing perspectives. Chapter 1 reviews the present body of knowledge regarding the social structure of female white-tailed deer, spatial patterns of dispersion, a relatively new model of population expansion, an alternate management strategy based on this model, the effects of social structure on the underlying genetic makeup of the population, and the utility of a new panel of genetic markers in this context.

Chapter 2 describes the sociospatial structure of female white-tailed deer on my study site in the central Appalachians. I assigned individuals to spatial groupings based on an extensive dataset of radiotelemetry-based locations and visual observations of associated does. Using genotype data from a panel of microsatellite loci, we used pair-wise genetic measures to evaluate the correspondence between spatial and genetic associations. To further investigate differences between our study population and those previously studied, I test the hypotheses that: 1) female white-tailed deer are not randomly distributed across the landscape, but are spatially grouped, and 2) these groups reflect genetic structuring of the population, such that individuals in close proximity to one another are more closely related than those in different spatial groups.

Chapter 3 examines microspatial genetic structure via a relatively new technique called spatial genetic autocorrelation analysis. Due to the lack of suitable genetic markers, microspatial assessment of genetic structure has not previously been used to characterize patterns of gene flow at the level of matriarchal groups for white-tailed deer.

Chapter 4 presents a retrospective assessment of the relatedness of white-tailed deer from an experimental removal. I used genetic information to assess the relatedness of the deer removed, as well as those remaining. The spatially-based removal also allowed me to genetically compare known fetus-dam pairs, thereby providing an estimate of the accuracy of my methods of parentage analysis. I discuss possible implications of my findings for the application of localized management in similar populations of white-tailed deer.

In Chapter 5, I conclude by summarizing the new findings and important differences in the social structuring of this population when compared to observations from other studies. Implications of these findings are discussed in the context of applying this information to alternate management strategies for overabundant deer populations. Manuscripts based on chapters 2 and 3 will be submitted to the *Journal of Wildlife Management,* and chapter 4 to the *Wildlife Society Bulletin.*

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CHAPTER 2

SOCIOSPATIAL STRUCTURE AND GENETIC RELATEDNESS OF FEMALE WHITE-TAILED DEER IN THE CENTRAL APPALACHIANS[1]

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Abstract

We compared sociospatial and genetic structure of female white-tailed deer (*Odocoileus virginianus*) in a nonmigratory, high density population inhabiting a forested environment in the central Appalachian Mountains of West Virginia during 1999-2001. We delineated groups based on home range overlap and verified these classifications based on visual observations. We then used pair-wise genetic measures to evaluate the spatial and genetic relationships of female deer. Our results suggest that home range locations were not random across the landscape of our study area, but were clumped into groups of spatially tolerant individuals sharing common ancestry. Adjacent groups displayed considerable overlap with one another, patterns of home range position within these spatial groups were not apparent, and older does did not demonstrate home range exclusivity. We conclude that some sociospatial tendencies observed in low density populations may not occur at high population densities.

Key words: central Appalachians, genetic structure, *Odocoileus virginianus*, social structure, white-tailed deer

Introduction

In white-tailed deer (*Odocoileus virginianus*), the fundamental social organization is considered a dominance hierarchy, where dominance is directly related to age (Hirth 1977) and social status largely dictates individual behavior (Marchinton and Hirth 1984). Marchinton and Atkeson's (1985) application of the concept of facultative territoriality recognized the importance of spatial considerations on white-tailed deer sociobiology. The social structure and spatial relationships exhibited by female white-tailed deer have been attributed to matrilineal

kinship (Aycrigg and Porter 1997, Hirth 1977, Nelson and Mech 1981, Nixon et al. 1991, Ozoga et al. 1982). Specifically, female social structure is considered to be a matriarchal group composed of three to four generations of females and their offspring (Hawkins and Klimstra 1970, Mathews and Porter 1993). Early observations suggested that preference for a range might be transferred across generations, as parent/offspring home range affinity was observed to span three generations in some cases (Marchinton and Hirth 1984). While early research established the generalized female social structure, a series of studies conducted within an 252-ha enclosure at the Cusino Wildlife Research Station in Michigan investigated the spatial arrangement of home ranges within female social groups and established that female social structure affects spatial arrangement of home ranges (Ozoga et al. 1982, Ozoga and Verme 1984).

Using 30 years of observations from the Adirondack Mountains of New York, Mathews (1989) hypothesized that there were anti-predatory functions of home range location within female social groups. She predicted that dominant does (matriarchs) would occupy the most preferred position within a social group's home range, and that the matriarch's youngest daughters would be allowed to share this home range, exclusive of the matriarch's older daughters. Accordingly, home ranges of young does (<2 years old) almost completely overlapped the home ranges of older deer. Moreover, high levels of home range overlap among all individuals within a social group suggested that white-tailed deer in forested environments were more social than previously thought. While not definitively proving or disproving the anti-predator hypothesis, these results from the Adirondacks suggested that home ranges were not randomly located within social groups.

Subsequent investigations on the same study area in the Adirondacks compared sociospatial behavior among and within kin groups (Aycrigg and Porter 1997). Sociospatial

behavior at the group level was relatively rigid, whereas the sociospatial patterns of individuals within groups were more flexible. Specifically, groups in their study were relatively stable through time (with respect to membership), while variation in sociospatial behavior at the individual level was largely dependant on age and reproductive status. Both investigations (Mathews 1989, Aycrigg and Porter 1997) reported that older females (>5 years old) maintained relatively distinct home ranges from other individuals of the same age class, during which they frequently were clustered with younger females. Because these Adirondack deer were unhunted, Mathews (1989) concluded that an older age structure aided in social group formation and stability that resulted from very high levels of female philopatry. Further, based on this high philopatry and a matriarchal dominance structure, they predicted that individual home ranges within each social group were analogous to petals of a rose, where the matriarch was located in the middle with younger group members (daughters) forming adjacent and overlapping home ranges radiating away from the matriarch's. These observations provided the basis for a model of deer population expansion called the "rose-petal hypothesis" (Porter et al. 1991). This model predicts that in populations exhibiting high female philopatry and low female dispersal, deer are spatially arranged at the landscape level as female family units with discrete home ranges. Subsequent research suggested that the radiocollared animals within social groups were more related to one another than to members of other groups, further supporting the model (Mathews and Porter 1993).

Although observations over the past two decades have shed considerable light on the role of sociobiology on spatial structure of female white-tailed deer in captive and/or migratory populations, little is known about the actual sociospatial structure in other contexts. Furthermore, effects of sociospatial structure on underlying genetic structure have been limited

by the ability to measure genetic variation on a sufficiently fine scale (Mathews et al. 1997). As in many populations in the northern parts of the species' distribution, the population in the Adirondack studies was seasonally migratory. Population density was low and social groups maintained relatively distinct group home ranges on summer range, while several groups might congregate in winter yards (Tierson et al. 1985). However, in much of eastern North America, particularly the Mid-Atlantic, Southeast, and lower Midwest, white-tailed deer are non-migratory and density of many populations is moderately to very high. Because conclusions based on the study of one population may not always be applicable to others (Miller 1997), results from the study population in the Adirondacks may not be applicable in other dissimilar areas of the eastern United States.

Present sociospatial models predict that the oldest female (the matriarch) in a social group will inhabit the central position within a relatively discrete, exclusive group, and would be surrounded by her descendants. The matriarch's high spatial tolerance of her younger offspring (fawns and yearlings), and reduced spatial tolerance of older offspring should produce detectable patterns of home range position relative to the entire group. Our objectives were to describe the sociospatial characteristics of groups of female white-tailed deer in a nonmigratory population in the central Appalachians. Utilizing genetic data and an extensive telemetry dataset, we compared sociospatial structure of a high-density herd with a heavily male-biased harvest history to that originally described in migratory, low-density populations.

Study Area

Our study was conducted on MeadWestvaco's 3,360-ha Wildlife and Ecosystem Research Forest (MWWERF), located in Randolph County, West Virginia (38°42'N, 80°3'W). Established in 1994, the MWWERF facilitates the study of industrial forestry's influences on

ecological and ecosystem processes in the central Appalachians. The MWWERF is located within the Unglaciated Allegheny Mountains and Plateau Physiographic province (Smith 1995), and is characterized by steep slopes, broad plateau-like ridge tops, and deeply incised valleys. Elevations on the MWWERF range from 700 to 1200 m and forest cover is predominantly an Allegheny-northern hardwood forest type. American beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and black cherry (*Prunus serotina*) are the predominant tree species. In addition, species from the mixed mesophytic forest type including yellow-poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), American basswood (*Tilia americana*), and black birch (*B. lenta*) are interspersed throughout much of the site. Rosebay rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) dominate the shrub layer throughout. The highest elevations support communities dominated by red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). As an artifact of high deer herbivory pressure and past forest management activities, understories of hay-scented fern (*Dennstaedtia punctilobula*) dominate throughout.

A detailed investigation of the deer herd on the MWWERF began in 1999, and >50% of deer on the site were marked with ear-tags or radio-collars. Pre-harvest deer densities and sex ratios during the study were estimated at 12-20 deer/km^2 and 6-18 adult males:100 adult females, respectively (Langdon 2001). Past abomasal parasite counts suggested the herd is at or near nutritional carrying capacity (Fischer 1996). In a concurrent study, Campbell et al. (2004a) observed very little seasonality with regard to home range position and reported high levels of philopatry of females on the study area, based on lack of dispersal and home range comparison among years.

Methods

Deer Capture

We captured deer from January to April 1999-2001 using modified Clover traps (Clover 1954) and rocket nets (Hawkins et al. 1968) baited with whole kernel corn. Captured deer were immobilized with 2.2 mg xylazine hydrochloride/kg body weight, followed by reversal via yohimbine hydrochloride (½ intravenous and ½ intramuscular at 0.3 mg/kg body weight). Deer ages were estimated using tooth eruption, wear, and replacement (Severinghaus 1949). All deer were ear-tagged and females radio-instrumented with a 3-year collar (Advanced Telemetry Systems, Isanti, MN, USA).

Radiotelemetry and Home Range Estimation

We collected radiotelemetry data year-round throughout the 24-hour day, 3-4 times per week, from permanently located and geo-referenced telemetry stations. We estimated deer locations using radio receivers and 4-element Yagi antennae. After taking 3-8 preliminary azimuths to pinpoint deer locations, we recorded two simultaneous azimuths that produced an angle of $90 \pm 40°$. We used CALHOME (Kie et al. 1996) to generate UTM coordinates of estimated deer locations. To reduce the effects of autocorrelation, $\geq$10 hours separated any two relocations of the same animal.

We assessed radiotelemetry error by randomly placing transmitters at geo-referenced stations (White and Garrott 1990). Each observer recorded azimuths from 5 different telemetry stations. Mean bearing error was –0.65° (SD = 8.41°) throughout the study, suggesting minimal bias in the telemetry protocol. Mean distance from estimated deer location to observer was 352.8 m, resulting in an estimated mean location error of 52.2 m (Campbell et al. 2004b). We

omitted all estimated locations in which the distance between the observer and the estimated deer location was ≥3 km.

We used the Animal Movements extension (Hooge and Eichenlaub 1997) of ARCVIEW® (Environmental Systems Research Institute 1999) to generate 95% home range area and activity center (home range centroid) estimates via the fixed kernel method with ad hoc calculation of a smoothing parameter (Worton 1989). All females with ≥20 radiotelemetry locations were included in the analysis. We used ARCVIEW® (Environmental Systems Research Institute 1999) and MeadWestvaco's Forest Research Information System (FRIS®) to overlay home ranges and activity centers onto a coverage map of the MWWERF. For each doe-pair having home range overlap, degree of overlap and distance between activity center was measured to aid in analysis of spatial association versus age and relatedness.

Group Delineation

Groups were identified based on home range overlap. We expressed degree of home range overlap for each possible pair of animals using Cole's coefficient of association (Cole 1949). We used the program NTSYS (Rohlf 1998) to perform cluster analysis based on the unweighted pair group method to aggregate individuals based on Cole's coefficient. To assess the spatial significance of each group, we examined the relationship between group size (measured in number of radiotelemetered females per group) and composite group home range area. If the spatial groups designated by our cluster analysis were simply artifacts of our analysis, and lacked actual spatial clustering, we would expect to see strong positive correlation between the composite group home range size and number of females assigned to each group. Because the data were non-normal, we assessed correlation between number of females per group and composite group home range area via Spearman's rank correlation.

Using groups previously defined via cluster analysis, linear distance between individual home range activity centers and composite group activity center was used to test for patterns in individual home range position by age class. Due to a lack of normality, we tested for these patterns in individual distance from group activity center using a Kruskal-Wallis test for each age class. As maturation of young individuals might confound spatiotemporal relationships between social group members, age classes used in the analyses were age of the animal in the year being analyzed and were defined as 0 (fawn), 1 (yearling), 2, 3, 4, 5, and 6+ years of age. The influence of the loss of an animal from a social group on the movement patterns of remaining individuals within the population was considered negligible. In a complementary analysis, we used ARCVIEW® to plot home ranges by age to visually inspect home range overlap by age class.

Genetic Analyses

We collected tissue samples from a subset of all deer captured. In 1999, we collected blood samples via venipuncture and stored them in vaccum tubes (Vacutainer, Becton-dickson and Company, Franklin Lakes, N.J.) containing Longmire buffer (Longmire et al. 1997). We collected ear-notch and muscle tissue samples from deer in 2000 and 2001, respectively, and stored individually in 95% ethanol at 4°C. We isolated DNA using Quiagen® mini-spin columns per manufacturer's recommendations (Dneasy™ Tissue Kit; QUIAGEN Genomics Incorporated, Bothell, Wash.), except that tissue lysis was performed overnight. Fragment amplification and separation was performed at the University of Georgia's Integrated Biotechnology Laboratory and followed reaction conditions and a subset of 10 primers (Laseter 2004) described by Anderson et al. (2002). DNA fragments were quantified and analyzed with Genescan® software

and alleles were assigned using Genotyper® software (Applied Biosystems, Inc. Foster City, CA) followed by visual inspection and verification (DeYoung et al. 2003).

We used the program GenAlEx V 5.1 (Peakall and Smouse 2001) to calculate allelic frequencies, expected heterozygosity, and observed heterozygosity. Pair-wise relatedness was calculated via the methods of Peakall et al. (1995). We used Spearman's rank correlation coefficient r_s to measure the association between genetic distance and geographic distance, as well as between home range overlap and genetic distance.

Visual Observations

Dense cover in our study area usually inhibited our ability to observe direct interactions between deer, beyond simply recording the identity of marked animals in proximity to one another. Opportunistic visual observations of deer were recorded using 10x40 binoculars. Observational data included: (1) date and time of observation; (2) nearest geo-referenced telemetry station; (3) sex and age class of individuals; (4) size of group; and (5) ear-tag numbers, if present. Deer were considered associates if they were visually observed together (separated by $\leq$25 m, Aycrigg and Porter 1997).

Results

Home Range Analyses

We generated home ranges and activity centers based on 20,587 telemetry locations for the 127 females having sufficient radiotelemetry locations ($\geq$20) to be included in the spatial structure analyses. Of the 127 females included in the spatial structure analyses, complete genotypes were available for 56 females. Mean ($\pm$ SE) number of locations/deer/year was 77 $\pm$ 3 for all 127 females, and 86 $\pm$ 5 for the subset of 56 animals included in the genetic analyses.

Overall estimated mean age was 3.6 $\pm$ 0.1 years, whereas the oldest deer was estimated to be 9 years of age.

Among females with overlapping home ranges, average home range overlap was 20.7% in year 1, 18.6% in year 2, and 21.4% in year 3. Based on these average home range overlap values and coincident visible clusters on dendrograms of home range overlap (Fig. 2.1), we delineated spatial groups based on an overall home range overlap value of 20% (Fig. 2.1, vertical dashed line). Clusters containing animals with $\geq$20% overlap with all other animals in the cluster were designated as spatial groups (Fig. 2.2). A total of 12 groups containing 59 does in 1999, 109 in 2000, and 104 in 2001 were delineated. Of the 127 does included in the home range overlap analysis, 43 (34%) were radiomonitored all three years. Group membership was remarkably stable, as does present in multiple years were consistently assigned to the same groups. Spearman's rank correlation of 95% group home range area versus the number of radiocollared deer per group (Fig. 2.3) revealed a nonsignificant relationship (r_s = 0.28, p = 0.12), indicating that number of radiocollared deer and group area were largely independent. Comparison of individual activity center distance from group activity center for the 7 age classes indicated no relationship in individual position within the spatial groups with respect to age (H = 1.35, p = 0.97). Visual inspection of home range overlap for females within the seven age classes revealed no obvious relationship between home range juxtaposition and age, as those in the oldest age class ($\geq$6 years) overlapped one another as frequently as those in younger age classes. An average of 19 females $\geq$6 years old were present in each year; each of these females displayed home range overlap with an average of 4 other females in the same age class. Average home range overlap for those females $\geq$6 years old was 20.6% (nearly the same as for radiotelemetered females of all ages).

Genetic Analyses

Our analysis of 10 microsatellite loci revealed high polymorphism among the deer we examined; detailed results of the microsatellite analyses are reported in Laseter (2004). The size range and distribution of alleles for each locus was consistent with that found in previous studies (Anderson et al. 2002, DeYoung et al. 2003) and all individuals were characterized by a unique multilocus genotype. Spearman's rank correlation revealed a weak positive relationship between home range centroid distance and genetic distance for year 1 ($r_s = 0.24$, $p < 0.01$), year 2 ($r_s = 0.18$, $p < 0.01$), and year 3 ($r_s = 0.16$, $p < 0.01$). Home range overlap and genetic distance showed a stronger, negative relationship for year 1 ($r_s = -0.49$, $p < 0.01$), year 2 ($r_s = -0.53$, $p < 0.01$), and year 3 ($r_s = -0.58$, $p < 0.01$), which is to be expected since as home range overlap increases, genetic distance is expected to decrease.

Visual Observations

We recorded 9,658 visual observations of deer during the study. Of those, 2,300 were marked animals, of which 1,430 were positively identified. Overall, 47% of the observations were solitary; when deer were observed together, the mode was 2 individuals, though we recorded groups of up to 10 deer. No individually marked animals were observed associating with members of other groups.

Discussion

With the exception of temporary seasonal movements of a few animals, our study population displayed high site fidelity with regard to female home range position (Campbell 2004a). Population densities on our study site were 3-4 times that reported in the Adirondack studies (McNulty et al. 1997, Langdon 2001). The more traditional method of assigning individuals to groups based on summer and winter home range commonalities was not

appropriate in our nonmigratory study population. Due to high home range overlap among does and high population densities on our study site, almost all radiocollared animals had home range overlap with several other animals (Fig. 2.2). This suggested that animals that might not have frequent social interactions with other animals still displayed varying amounts of spatial tolerance of other animals.

Our results generally support previous descriptions of female white-tailed deer sociobiology, with notable exceptions attributable to behavioral plasticity in response to high population density. Consistent with the rose-petal hypothesis presented by Porter et al. (1991), groups of spatially tolerant, genetically related individuals appeared to occur across the landscape of our study area. Although elevated population density on our study area prevented the formation of exclusive group home ranges, we found evidence supporting the existence of spatial aggregations of females whose membership was stable during the study period. Stability of matrilineal groups over time has been attributed to the benefits derived from the presence of additional females in the vicinity (Aycrigg and Porter 1997). Additionally, familiarity with a geographical area is thought to enhance reproductive success. Younger females may also receive benefits, (high quality habitat, anti-predator functions, knowledge of local resources) by sharing ranges with older, dominant females (DeGayner and Jordan 1987).

Our findings deviate somewhat from the rose-petal model as formulated by Porter et al. (1991). If the rose-petal distribution holds, we would expect to see the older age classes correspond to the shortest distances (nearest to the group activity center), followed by the youngest animals at intermediate distances, and the older offspring of the matriarch at the greatest distance from the group activity center within each of our previously-defined spatial groups. Furthermore, exclusivity of group home ranges and spatial intolerance among older

females (matriarchs) would be expected. Matrilineal clusters of females existed on our study area; however two important attributes of these clusters differ from that predicted by the rose-petal hypothesis. We found no evidence that older females inhabited central positions within these spatial groups, nor did we find that older ($\geq$6 years) females maintained distinct home ranges from other older females. Aycrigg and Porter (1997) concluded that the exclusive ranges of older females in their study may have reflected social dominance. Even though no independent measure of dominance was available, this is consistent with observations of other species where age and dominance are directly related (Clutton-Brock et al. 1982, Franklin and Leib 1979). Previous investigations (Nelson and Mech 1984, Aycrigg and Porter 1997) have suggested that the lack of a detectable spatial pattern in home ranges of $\leq$5 year old deer means that younger, subordinate females may be unable to maintain exclusive home ranges. These sociospatial tendencies may deteriorate at some population density threshold. The higher population densities found on our study area may preclude the formation of exclusive home ranges for even the most senior matriarchs.

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Figure 2.1. Dendrogram representing the results of UPGMA cluster analysis on home range overlap for female white-tailed deer during 2001 on the MeadWestvaco Wildlife and Ecosystem Research forest in Randolph County, West Virginia. Despite the loss or addition of group members (by death or capture of additional animals), group membership (denoted by brackets and letters) remained remarkably stable among all three years. Based on home range overlap, females grouped together in one year were consistently in similar clusters in other years. The vertical dashed line shows the home range overlap value (20%) at which groups were delineated in all years.

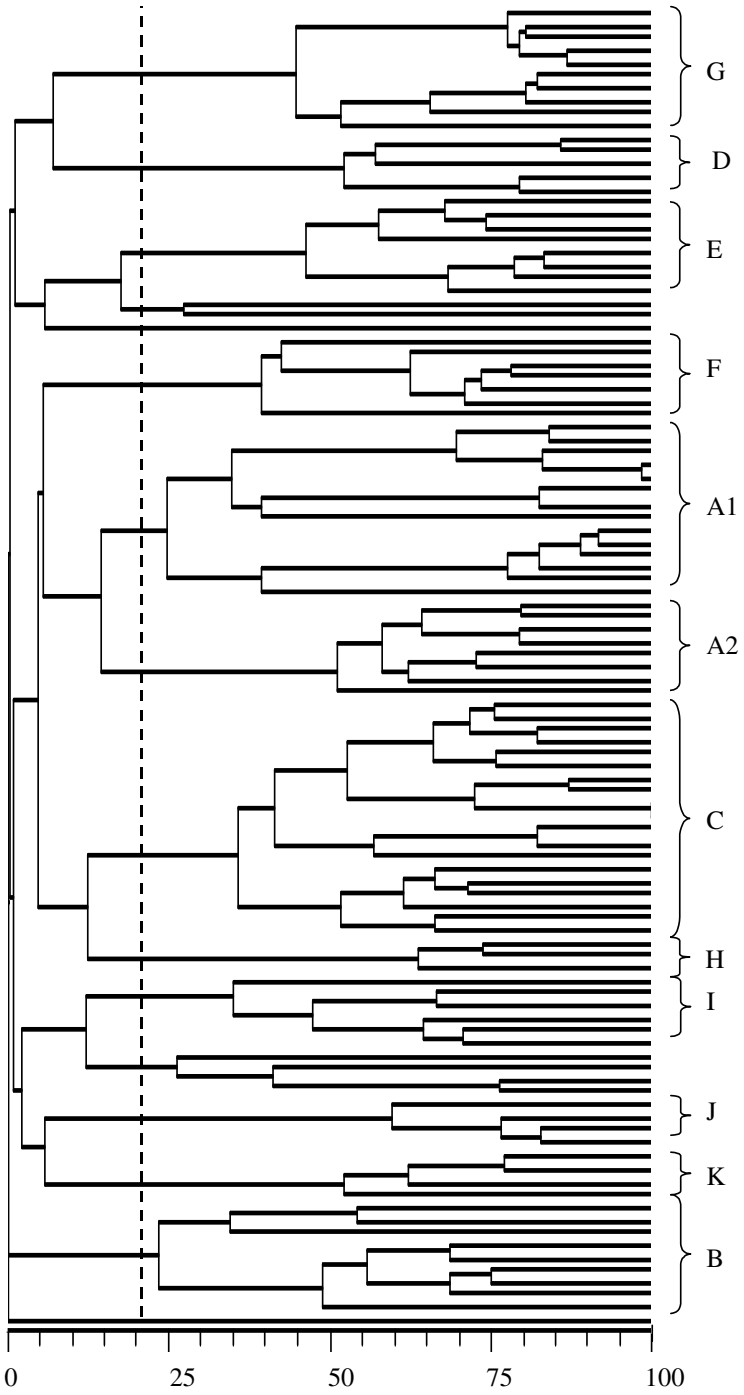

G
D
E
F
A1
A2
C
H
I
J
K
B
0
25
50
75
100
Percent Home Range (95% Kernel) Overlap

Figure 2.2. Composite home ranges for 12 groups including 127 female white-tailed deer monitored from 1999-2001 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia.

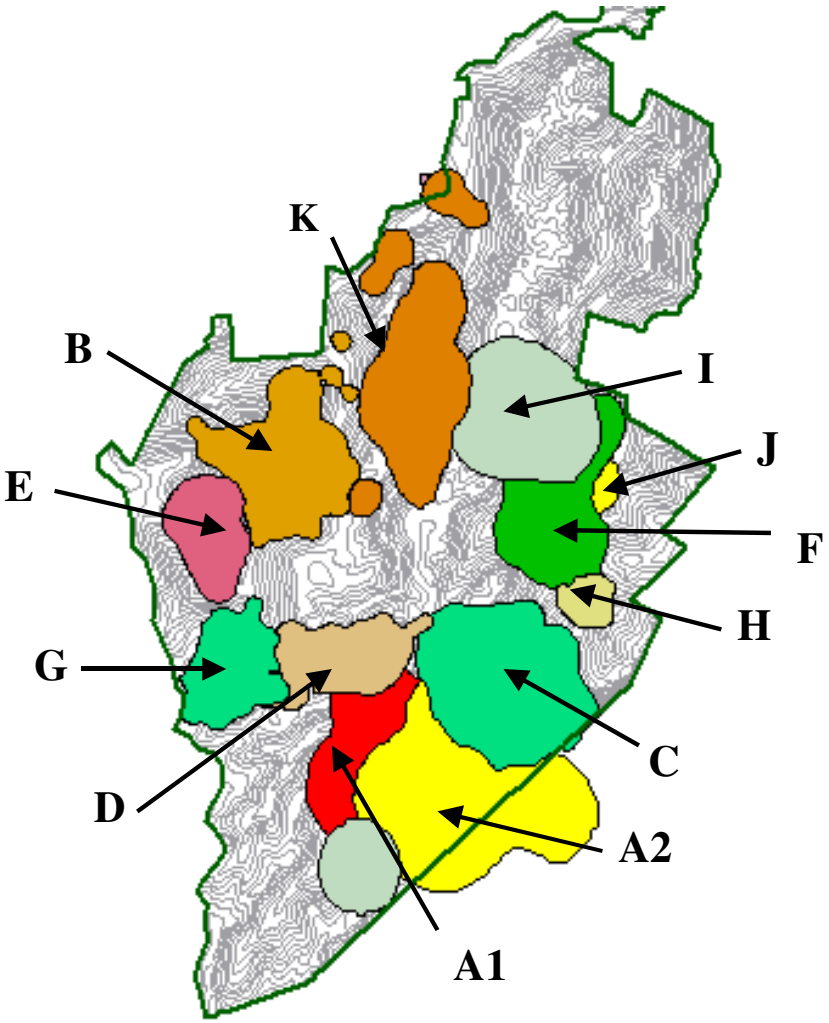
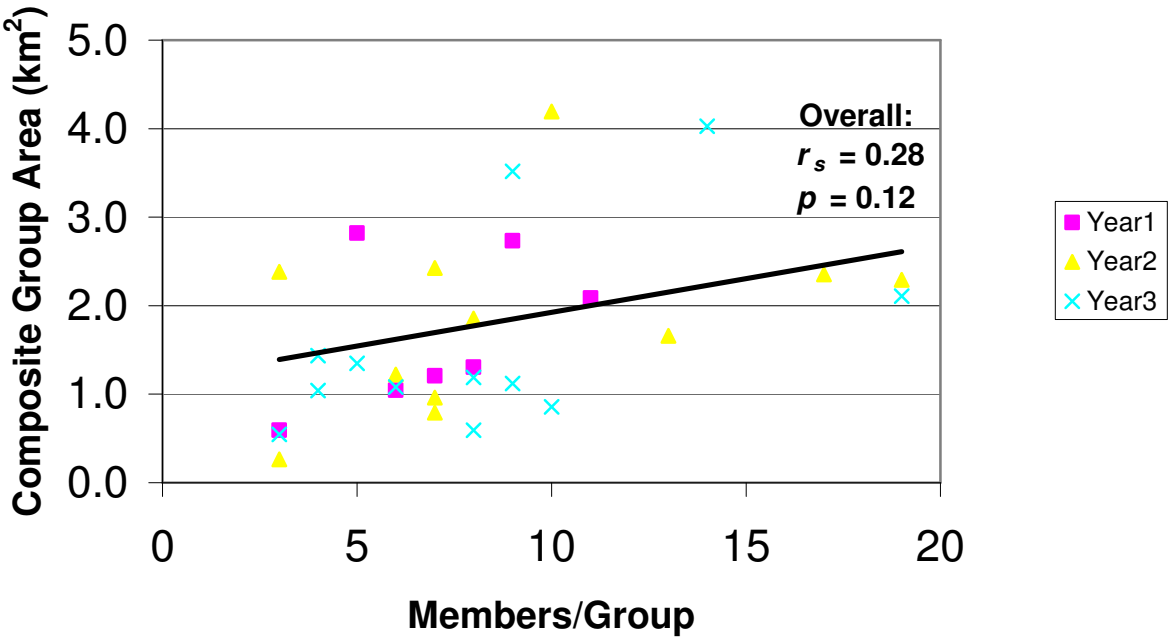

K
B
I
J
E
F
H
G
C
D
A2
A1

Figure 2.3. Spearman's rank correlation of 95% group home range area versus the number of radiocollared deer per group for 12 groups including 127 female white-tailed deer monitored from 1999-2001 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia. Number of radiocollared deer per group and composite group home range area were largely independent.


Composite Group Area (km²)
5.0
4.0
3.0
2.0
1.0
0.0
0
5
10
15
20
Members/Group
Overall:
r_s = 0.28
p = 0.12
Year1
Year2
Year3

CHAPTER 3

SPATIAL GENETIC AUTOCORRELATION OF FEMALE WHITE-TAILED DEER: SPATIAL GROUPS AS DEMES?[1]

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

Abstract

Despite numerous investigations of deer sociobiology and genetic attributes, the effects of social organization on genetic structure in white-tailed deer are not well understood. In addition to inherent differences among and within populations, the lack of suitable genetic markers has prevented microspatial assessment of genetic structure until recently. We coupled spatial autocorrelation analysis with a recently developed microsatellite panel to assess genetic structuring within a population of white-tailed deer (*Odocoileus virginianus*) during 1999-2001 in the central Appalachians of West Virginia. We found evidence for significant microspatial genetic structure among females on our study site, although groups of these females probably cannot be considered demes. Our results also suggest that population density will also influence the spatial scale at which genetic structure may be evident in a population. As population density increases, female groups become less spatially discrete, allowing higher levels of gene flow among groups.

Key words: central Appalachians, deme, genetic structure, *Odocoileus virginianus*, social structure, spatial genetic autocorrelation, white-tailed deer

Introduction

Geographic subdivision in mammalian genetic variation is common, and usually is the result of geographic or ecological barriers to gene flow that can result in the formation of geographic races distributed across a species' range (Mathews et al. 1997). The degree to which gene flow between populations is limited often determines the level of genetic diversity within

populations, as well as the genetic divergence between populations. Although both ecological and geographic barriers have long been known to limit gene flow, the effects of social organization on gene flow have only recently been explored.

The development of fine-scale (<1 km) spatial genetic structure is considered unlikely in widely dispersing animal taxa. Alternatively, groups such as small mammals that exhibit restricted dispersal are much more likely than larger mammals to exhibit local positive genetic structure (Peakall et al. 2003). Social organization rather than restricted dispersal *per se*, may also generate nonrandom genetic patterns. Scribner and Chesser (1993) showed that the spatial segregation of kin groups of the eastern cottontail (*Sylvilagus floridanus*) could create barriers to restrict gene flow, generating fine scale patchy distributions of genotypes. Different patterns of genetic structure between sexes can also be created in species exhibiting strong sex-specific philopatry (Chesser 1991a, b). van Staaden et al. (1996) observed a lack of short positive genetic structure in Richardson's ground squirrels (*Spermophilus richardsonii*), also suggesting social organization (rather than restricted dispersal) as the causative factor. Based on studies of Australian bush rats (*Rattus fuscipes*), Peakall et al. (2003) suggest that microscale genetic structure analysis is particularly promising in studies of small mammal dispersal, although the applicability of these analyses to philopatric, matriarchal groups of other mammalian species is obvious.

Many studies of macrogeographic genetic variation in white-tailed deer (*Odocoileus virginianus*) have successfully used allozymes, nuclear DNA, and mitochondrial DNA to investigate genetic subdivision (Ellsworth et al. 1994). These studies have investigated different aspects of geographic variation on larger scales, while few have investigated genetic variation at the microscale (Mathews 1989, DeYoung et al. 2003). Theoretically, social organization affects

patterns of genetic variation within and between social groups (Chesser 1991a), however markers suitable for these analyses have not been available until recently (Anderson et al. 2002, DeYoung et al. 2003). To investigate patterns of genetic variation at the level of the social group and its constituent individuals, genetic markers with high levels of genetic polymorphism on a microgeographic scale are required.

White-tailed deer in forested environments form matrilineal groups (Tierson et al. 1985, Mathews 1989, Aycrigg and Porter 1997), usually composed of adult females, several generations of female offspring, and young males who have not yet dispersed (Hawkins and Klimstra 1970, Hirth 1977, Nelson and Mech 1984, Aycrigg and Porter 1997). Furthermore, these studies have suggested that the members of these matrilineal groups associate throughout the year. Female dispersal is generally low (5-20%), whereas male dispersal is relatively high (>85%) (Hawkins and Klimstra 1970, Hirth 1977, Tierson et al. 1985, Nelson and Mech 1987, Mathews 1989, Nelson 1993). These sociospatial attributes (matriarchal organization, philopatry, limited female dispersal) suggest that white-tailed deer are well suited for studies of microgeographic genetic variation.

Previous studies documented genetic sub-structuring within deer populations, but on larger geographic scales (Sheffield et al. 1985, Kennedy et al. 1987). These studies also concluded that deer populations across their respective areas contained numerous functional genetic subpopulations. Nelson and Mech (1987) suggested that deer from separate winter yards in northeastern Minnesota represented subpopulations that constituted genetic demes. Adult deer from each winter yarding area occupied summer ranges exclusive of deer from neighboring yards. These relationships were predicted to persist as adult movement patterns were traditional. Most yearling females established home ranges on or near their birth ranges and continued the

migration pattern of their mothers. This tendency was further expected to lead to breeding between fathers and daughters as the same dominant bucks were expected to maintain breeding tenure on their ranges for >1 year. Female philopatry was also suggested to lead to inbreeding with brothers and other close kin in instances where males never dispersed from their natal ranges. Nelson and Mech's (1987) observations were based on four deeryards separated by a minimum of 10 km in an area where deer densities were estimated between 0.2 and 0.4 deer/km^2. Although genetic data were not available to test their hypothesis of populations consisting of conglomerates of demes, data from other species and populations are supportive. Significant differences in gene frequency were found between upland and lowland white-tailed deer in South Carolina (Manlove et al. 1976, Ramsey et al. 1979, Chesser et al. 1982b), among moose subpopulations (*Alces alces*, Chesser et al. 1982a), and subgroups of other large mammals including red deer (*Cervus elaphus*, McDougall and Lowe 1968, Gyllensten et al. 1980), reindeer (*Rangifer tarandus*, Braend 1964), and elephant (*Loxodonta africana*, Osterhoff et al. 1974).

Mathews (1989) and Mathews and Porter (1993) investigated the relationships between social structure, genetic structure, and geographic location among social groups of white-tailed deer in the Adirondack Mountains of New York. They tested the hypothesis that social structure had produced genetic structure, evidenced by a greater amount of genetic variability among groups than within groups. Despite using less variable markers (allozymes) than those currently available today (i.e., microsatellites), Mathews (1989) found that social groups were genetically distinct units and that a significant amount of the genetic variability on her 60km^2 study area was accounted for by social groups.

The low-density, seasonally migratory populations in Minnesota and New York maintained separate summer and winter ranges, while some degree of overlap existed on summer

range, providing the opportunity for genetic exchange between adjacent social groups (Nelson and Mech 1987, Mathews and Porter 1993). Evidence from the nonmigratory population we studied in the central Appalachians (Laseter 2004) suggests that in high density populations, adjacent social groups do not maintain discrete group boundaries and may tolerate significant homerange overlap with members of other groups. High amounts of inter-group overlap might be expected to promote genetic interchange among groups, hence minimizing genetic structure. The social factors influencing microspatial genetic structure in white-tailed deer are not well understood. Thus it is unclear whether migratory tradition, population density, or some other factor is the primary influence genetic structure.

Our objective was to assess the level of spatial and genetic structure to determine the potential of deme formation on a microgeographic scale in a nonmigratory, high density population of white-tailed deer in the central Appalachian mountains of West Virginia. Our analysis is one of the first to employ spatial autocorrelation analysis via microsatellite markers for the purpose of elucidating microspatial genetic structure associated with social groups of white-tailed deer. The high level of genetic resolution possible with microsatellite markers, along with the increased sensitivity of spatial autocorrelation analysis provide discriminatory power not previously available.

Study Area

Our study was conducted on MeadWestvaco's 3,360-ha Wildlife and Ecosystem Research Forest (MWWERF), located in Randolph County, West Virginia (38°42'N, 80°3'W). Established in 1994, the MWWERF facilitates the study of industrial forestry's influences on ecological and ecosystem processes in the central Appalachians. The MWWERF is located within the Unglaciated Allegheny Mountains and Plateau Physiographic province (Smith 1995),

which is characterized by steep slopes and narrow valleys. Elevations on the MWWERF range from 700 to 1,200 m and forest cover is predominantly an Allegheny-northern hardwood forest type but also includes species from the mixed mesophytic forest type. As an artifact of high deer herbivory pressure and past forest management activities, understories of hay-scented fern (*Dennstaedtia punctilobula*) dominate throughout.

A detailed investigation of the deer herd on the MWWERF began in 1999. Approximately 52% of deer on the site were marked with ear-tags or radio-collars (Langdon 2001). Pre-harvest deer densities and sex ratios during the study were estimated at 12-20 deer/km^2 and 6-18 adult males:100 adult females, respectively (Langdon 2001). Abomasal parasite counts suggest the herd is at or near nutritional carrying capacity (Fisher 1996). In a concurrent study, Campbell et al. (2004a) found that few (<5%) radiotelemetered female deer on the MWWERF exhibited bimodal home ranges. Additionally, dispersal was observed in <4% of female fawns, while no deer ≥1 year old dispersed (Campbell et al. 2004).

Methods

Deer were captured from January to April 1999-2001 using modified Clover traps (Clover 1954) and rocket nets (Hawkins et al. 1968) baited with whole kernel corn. We immobilized deer with xylazine hydrochloride (2.2 mg /kg body weight), followed by reversal via yohimbine hydrochloride (½ intravenous and ½ intramuscular at 0.3 mg/kg body weight). We estimated age following (Severinghaus 1949). All deer were ear-tagged and all females were instrumented with a 3-year radio collar (Advanced Telemetry Systems, Isanti, MN, USA).

Radiotelemetry and Home Range Estimation

Radiotelemetry data were collected year-round throughout the 24-hour day from permanently located and geo-referenced telemetry stations. We estimated deer locations using

radio receivers and 4-element Yagi antennae. Following 3-8 preliminary azimuths to pinpoint deer locations, we recorded two simultaneous azimuths that produced an angle of 90 $\pm$ 40°. We generated UTM coordinates of estimated deer locations using CALHOME (Kie et al. 1996). To assure independence, $\geq$10 hours separated any two relocations of the same animal.

We assessed radiotelemetry error by randomly placing transmitters at geo-referenced stations (White and Garrott 1990). Mean bearing error was –0.65° (SD = 8.41°) throughout the study, suggesting minimal bias in the telemetry protocol. Mean distance from estimated deer location to observer was 352.8 m, resulting in an estimated mean location error of 52.2 m (Campbell et al. 2004). We omitted all estimated locations in which the distance between the observer and the estimated deer location was $\geq$3 km.

We used the Animal Movements extension (Hooge and Eichenlaub 1997) of ARCVIEW® (Environmental Systems Research Institute 1999) to generate 95% home range and activity center (home range centroid) estimates based on all radiotelemetry locations via the fixed-kernel method with ad hoc calculation of a smoothing parameter (Worton 1989) for all females with $\geq$20 locations. We used ARCVIEW® (Environmental Systems Research Institute 1999) and MeadWestvaco's Forest Research Information System (FRIS®) to overlay activity centers onto a coverage map of the MWWERF.

Genetic Analyses

Tissue samples were collected from a subset of all deer captured. In 1999, blood samples were collected by venipuncture and stored in vaccum tubes (Vacutainer, Becton-dickson and Company, Franklin Lakes, N.J.) containing Longmire buffer (Longmire et al. 1997). Ear-notch and muscle tissue samples were collected from deer in 2000 and 2001, respectively, and stored individually in 95% ethanol at 4°C. We isolated DNA using Quiagen® mini-spin columns per

manufacturer's recommendations (Dneasy™ Tissue Kit; QUIAGEN Genomics Incorporated, Bothell Wash.), except that tissue lysis was performed overnight.

Fragment amplification and separation was performed at the University of Georgia's Integrated Biotechnology Laboratory and followed reaction conditions and a subset of 10 primers (Laseter 2004) described by Anderson et al. (2002). DNA fragments were quantified and analyzed with Genescan® software and alleles were assigned using Genotyper® software (Applied Biosystems, Inc. Foster City, CA) followed by visual inspection and verification (DeYoung et al. 2003).

Statistical Analyses of Spatial Genetic Structure

We used the program GenAlEx V 5.1 (Peakall and Smouse 2001) to calculate allelic frequencies, expected heterozygosity and observed heterozygosity and to perform spatial autocorrelation analysis and matrix correlation analysis on the 56 radiotelemetered females for which genetic data were available. Spatial autocorrelation analysis addresses the question of geographic independence of similar genotypes within a given spatial scale. The null hypothesis is that genetic similarity and geographic proximity are independent of one another. As modified by Smouse and Peakall (1999) for multiallelic codominant, multilocus panels of genetic markers (i.e., microsatellites), this multivariate approach to autocorrelation analysis provides a method to investigate fine-scale patterns of spatial genetic structure not previously accessible. Pairwise individual-by individual genetic distances for each locus were calculated by GenAlEx via methods of Peakall et al. (1995); linear pairwise geographic distances were calculated as the Euclidean distance between x- and y- coordinates. To complement spatial autocorrelation analysis, we used a Mantel test (Mantel 1967) to measure the correspondence between the geographic and genetic distance matrices.

Results

Genetic and radiotelemetry data were available for 56 females. Mean (±SE) number of locations/deer was 189±15. Our analysis of the 10 microsatellite loci revealed high polymorphism among the deer we examined (*k* range: 4-17; *x*=10.0). The size range and distribution of alleles for each locus was consistent with that found in previous studies (Anderson et al. 2002, DeYoung et al. 2003, Laseter 2004). Expected heterozygosity was 0.71 and mean PIC = 0.67. All individuals were characterized by a unique multilocus genotype.

We found significant spatial structure for the shortest distance classes (Fig. 3.1), as shown by *r*-values exceeding the 95% upper confidence limits. The curve first crosses the x-axis at 478 meters, providing an estimate of spatial extent of genetic substructure (Sokal and Wartenberg 1983). After a brief distance of significantly positive *r*-values between 650 and 800 meters, the curve returns to nonsignificant values and oscillates within the confidence interval, consistent with a pattern of strong microspatial structure (Smouse and Peakall 1999). Our null hypothesis of no spatial genetic clustering is clearly rejected, and positive structure is apparent for the shorter (<500m) distance classes. The Mantel test of matrix correspondence indicated that the correlation between the elements of both matrices was r = 0.659 ($P \leq 0.01$), indicating that pair-wise genetic and geographic distances were positively but not strongly correlated with one another.

The correlogram of spatial autocorrelation (Fig. 3.1) indicates that the approximate scale of spatial genetic structure of the 56 genotyped individuals was 500 meters. Assuming the spatial scale of microgeographic variation on our study site was approximately 500 meters (inferred matriarchal group), we overlaid 500m-radius circles on obvious aggregations of home range activity centers within the MWWERF (Fig. 3.2). Given the apparent spatial clustering of

home range activity centers indicated, we tested for genetic differentiation among these putative spatial groups of animals. Using the AMOVA function within GenAlEx, which follows Michalakis and Excoffier (1996) to calculate a multilocus microsatellite F_{ST}, we determined that 5% of the relative variability among the deer we sampled was accounted for by variability among spatial groups ($F_{ST} = 0.050$, $P \leq 0.01$).

Discussion

We reject our null hypothesis of a random distribution of genotypes within this population of female white-tailed deer. The spatial genetic autocorrelation analysis indicated that proximate female white-tailed deer are more similar genetically than more distant animals. Moreover, evidence exists for a series of clustered distributions of like genotypes at a microspatial scale consistent with matriarchal groups.

Based on our combined analyses, detectable positive spatial genetic structure was well within the scale of our study area. Models of restricted gene flow, regardless of the source of the restriction (geographic, social, etc.), predict a pattern of genetic structure characterized by initial positive autocorrelation that declines through zero, becomes negative, and is then often followed by oscillation of positive and negative values (Peakall et al. 2003). We observed the pattern in this investigation, confirming that the spatial scale of our sampling encompassed the extent of positive genetic structure. The oscillation in our genetic autocorrelation supports our conclusion that the extent of positive genetic structure was captured within our sampling scheme. The Mantel test further confirmed our conclusion. Detection of a strong relationship between genotypic and geographic distance via a Mantel test is unexpected, unless the signal is strong across the whole dataset (Peakall et al. 2003). In contrast to our study, strong relationship across

an entire dataset would suggest that the full extent of spatial autocorrelation has not been completely represented.

Following the intersection of the *r*-value curve with the x-axis at 478m in our correlogram (Fig. 2.1), our results indicate a return to significant spatial genetic autocorrelation at values between 650 and 800 meters. The cause of this "spike" in positive correlation is uncertain, but may be due to stochastic variation in genetic or spatial structure. Also possible are unforeseen sampling effects inherent in our study design. Mathews et al. (1997) suggested that past fissioning of groups along matrilines may have confounded analysis of genetic versus spatial proximity of social groups in their study. Over a period of time, older but subdominant females leave social groups to become the matriarch of their own group as has been documented in red deer (Clutton-Brock 1989) and in rhesus monkeys (*Macacca mulatta*, Chepko-Sade and Sade 1979). If the founding member of these new groups disperses farther than less related existing groups, spatial proximity will no longer reflect genetic similarity among social groups within a given population. The spatial genetic correlation between 650 and 800 meters may be reflective of the fissioning of matriarchal groups and the establishment of home range activity centers away from their natal social group.

Nelson and Mech (1987) observed that social groups constituted genetic demes, with little genetic interchange among groups. They hypothesized that wintering yards were the focal points of demes, based on habitat use, but were not able to test the hypothesis genetically. Considering the low population density in their study (0.2 – 0.4 deer/km^2), the distance between groups was larger than the average male dispersal distance. Their groups may have constituted genetic demes simply by virtue of their geographic separation, and were an artifact of a sparse population of deer being clumped by social (matrilineal) affiliation across the landscape.

Our analyses also indicate that genetic structure is present within our study population (F_{ST} =0.050, $P \leq 0.010$), however the levels of genetic variation explained by spatial groups were less than half compared to those reported in the Adirondacks (F_{ST} =0.120, $P \leq 0.100$). We believe these lower (but statistically significant) values reflect differences in spatial structure on our study site. Population densities on our study site were 3-4 times greater than that reported in the Adirondack studies (McNulty et al. 1997, Langdon 2001). It appears that higher white-tailed deer population densities have facilitated greater overlap among adjacent social groups.

We find that in white-tailed deer, per-generational gene flow is sufficiently restricted to generate positive local genetic structure. In the absence of any other factor limiting gene flow, strong philopatric tendencies explain this finding. The relatively low (albeit significant) levels of genetic differentiation between groups of deer are likely products of higher population density facilitating extensive home range overlap among individuals and groups.

Restricted per-generational dispersal can result in strong local genetic structure (Peakall et al. 2003), while evolutionary estimates of gene flow, such as F_{ST}, may indicate higher gene flow at a much larger scale. Both of these observations are consistent with the results from our study and suggest that small family groups are producing the local genetic structure we found, while gene flow in an evolutionary context is widespread across the landscape of our study area. Barring geographical barriers to gene flow, we predict that deme formation in the central Appalachians is unlikely at population densities comparable to those on our study site.

Management Implications

Our results support the existence of microspatial genetic structure within white-tailed deer populations. The genetic structure we observed in this study is likely a consequence of spatial fidelity of matrilineal groups. Microsatellite DNA markers coupled with spatial genetic

autocorrelation analysis provided resolution not previously reported in investigations of white-tailed deer sociobiology. Genetic analyses indicated that the spatial scale of genetic structure in our study population was approximated by circular areas with 500m radius. Our findings also suggest that high population density promotes higher genetic exchange between matrilineal groups, even in populations exhibiting high female philopatry and low female dispersal. As with other behavior-based theories, the inherent behavioral plasticity of this species must be considered when generalizing social and genetic attributes in varying contexts.

Acknowledgements

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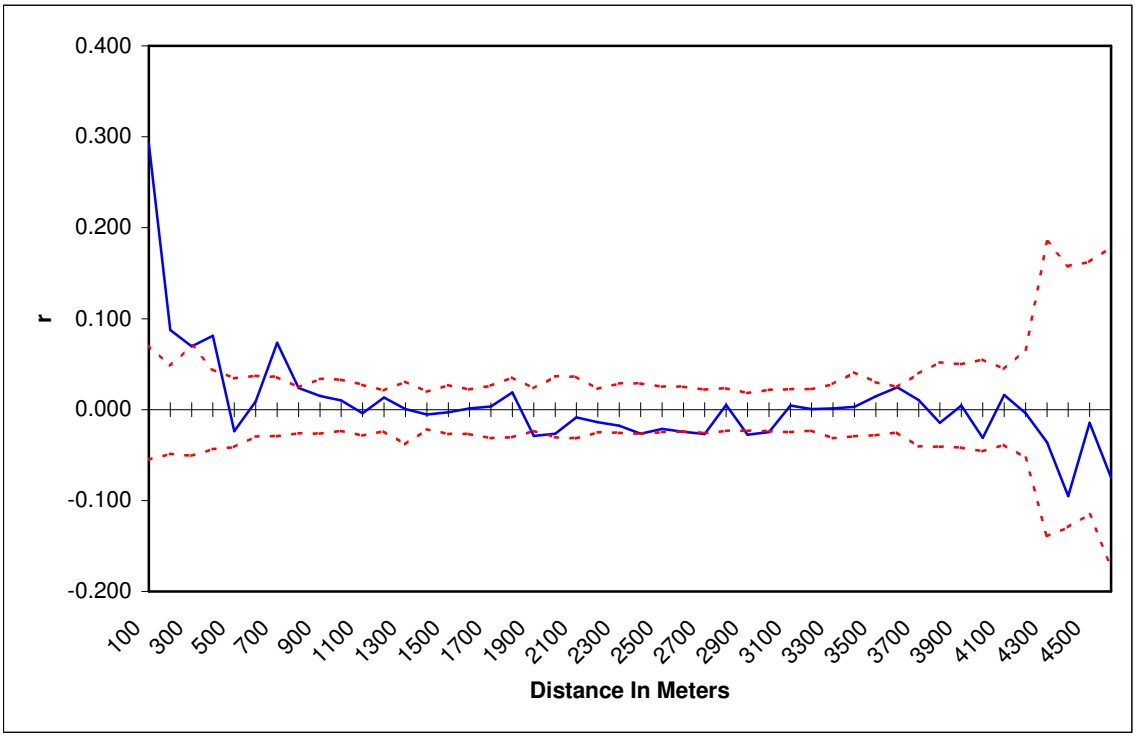
Figure 3.1. Correlogram showing combined genetic correlation (r, solid line) as a function of distance for 56 female white-tailed deer monitored during 1999-2001 on the MeadWestvaco Wildlife and Ecosystem Research forest in Randolph County, West Virginia. Dotted lines represent 95% CI about the null hypothesis of a random distribution of genotypes.


0.400
0.300
0.200
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0.000
-0.100
-0.200
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2100
2300
2500
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2900
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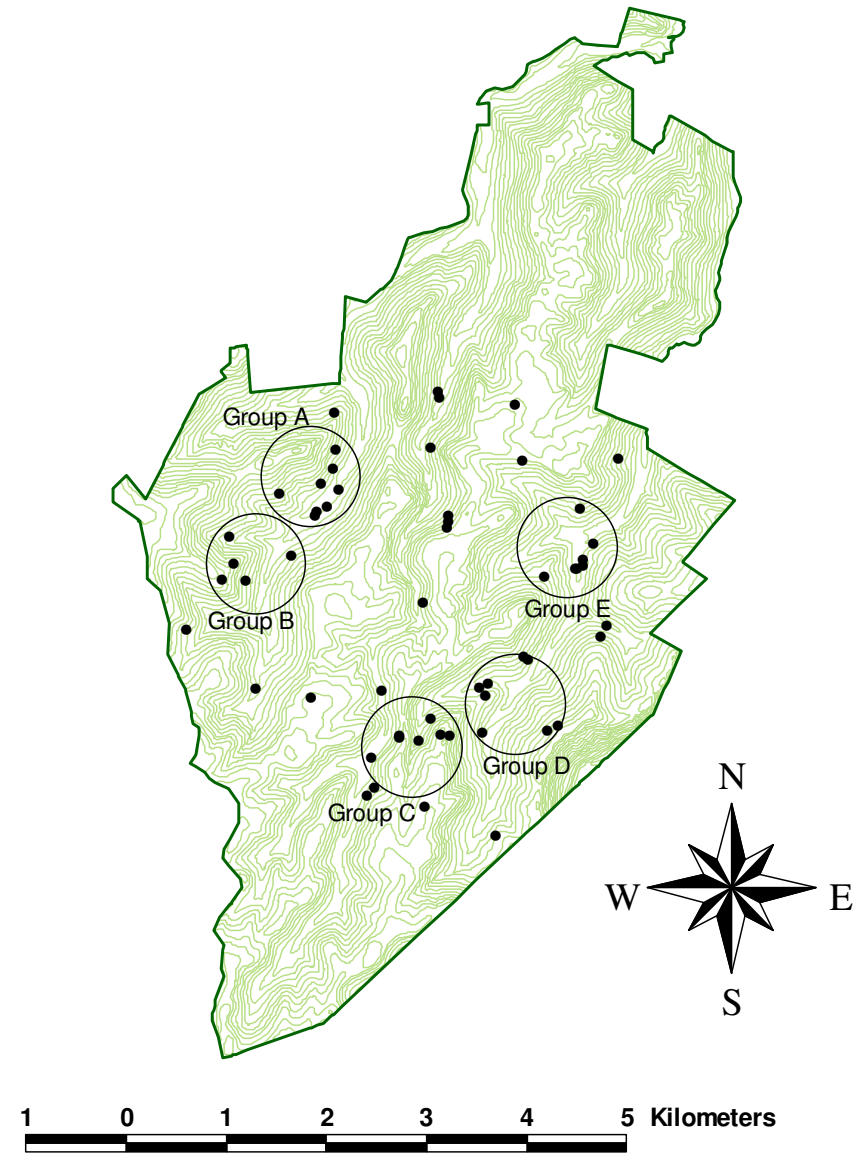
3900
4100
4300
4500
Distance In Meters

Figure 3.2. Home range activity centers (indicated by dots) for 56 female white-tailed deer monitored during 1999-2001 on the MeadWestvaco Wildlife and Ecosystem Research forest in Randolph County, West Virginia. Circles have a radius of 500m and approximate the likely scale of spatial genetic structure on our study site.


Group A
Group B
Group C
Group D
Group E
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S
1 0 1 2 3 4 5 Kilometers

CHAPTER 4

RETROSPECTIVE ASSESSMENT OF THE RELATEDNESS OF WHITE-TAILED DEER FROM AN EXPERIMENTAL REMOVAL[1]

[1] Laseter, B. R., T. A. Campbell, K. V. Miller, and W. M. Ford. To be submitted to *Wildlife Society Bulletin*

Abstract

Localized management, a nontraditional management strategy based on social structure of white-tailed deer (*Odocoileus virginianus*) has been suggested as an alternate management strategy on a variety of deer population scenarios and landscapes. Past evaluations of this strategy have lacked genetic information of sufficient resolution to adequately assess the relatedness both of the deer removed and those remaining. We conducted an experimental removal designed to mimic the practical application of localized management. Our objectives were to evaluate a genetic marker panel in the context of a group of closely related individuals, and to use this genetic information to retrospectively assess the relatedness of deer from an experimental removal. We collected 12 bucks, 39 does and 42 fetuses to assess the accuracy of a panel of 10 microsatellite loci, and subsequently tested the relatedness of deer removed from the 1.1 km^2 removal area in the central Appalachians of West Virginia in 2002. This panel of microsatellite loci was highly accurate, correctly assigning parentage for 41 of 42 fetuses collected from a local group of does. Genetic analysis of the removal deer revealed that the majority were closely related to others included in the removal. Our data also suggest that while the patterns of inter-relatedness observed in our study are consistent with matriarchal social structure reported in previous studies, higher population density may affect the composition of deer groups removed in spatially-based localized management efforts. Specifically, matriarchal groups may not maintain exclusive ranges at high densities such that localized areas contain several overlapping groups. The lack of spatial exclusivity of matriarchal groups suggests that rapid recolonization may jeopardize the intended effects of localized management efforts.

Key words: DNA microsatellites, localized management, matriarchal groups, white-tailed deer, West Virginia

Introduction

In forested environments of eastern North America, white-tailed deer (*Odocoileus virginianus*) form matrilineal groups, usually composed of older females and their female offspring (Hawkins and Klimstra 1970, Hirth 1977, Nelson and Mech 1984, Aycrigg and Porter 1997). In populations where females exhibit high site fidelity and low dispersal rates, it is traditionally assumed that does and their offspring form stable, persistent matriarchal groups whose members associate throughout the year (Tierson et al. 1985, Mathews 1989). Although the social organization of white-tailed deer has been investigated in a variety of populations (Hawkins and Klimstra 1970, Hirth 1977, Nelson and Mech 1981, Mathews and Porter 1993, Ozoga et al. 1982), many attributes have been difficult to generalize as behavioral plasticity varies by population demographics, habitat, and geographical region (Marchinton and Hirth 1984, Marchinton and Atkeson 1985). Nonetheless, understanding the degree of this plasticity is increasingly important as managers consider behavior-based management strategies (Miller 1997).

Overabundant white-tailed deer can alter forested ecosystem processes and can have deleterious effects on forest regeneration and the ecological integrity of forests in general (Tilghman 1989). Localized management is an alternate concept of deer population management that entails the removal of all animals within an entire social group within discrete, small geographic areas (Porter et al. 1991). This alternate method employs a localized removal of deer rather than a widespread reduction in population density in order to alleviate locally detrimental

environmental impacts associated with high deer densities. Porter et al. (1991) further generalized that in populations exhibiting high female philopatry and low female dispersal, a localized removal of deer could provide a persistent (>10 years) zone of low deer density. Recent examinations of female white-tailed deer movement have suggested that localized management could be a viable management tool to control herbivory at a local scale (Kilpatrick and Spohr 2000, Grund et al. 2002, Porter et al. 2004). Moreover, the work suggests that localized management theoretically could be effective throughout a spectrum of population densities (Porter et al. 1991). Still, definitive information across a wide range of population densities currently is lacking as these theories remain largely untested outside the Adirondack Mountains (McNulty et al. 1997, Oyer and Porter 2004). Based on an unhunted, seasonally migratory, low-density population, McNulty et al. (1997) targeted a social group of 17 does; 14 were successfully removed. Oyer and Porter (2004) subsequently monitored the removal area created by McNulty et al. (1997) to assess the persistence of the localized reduction in deer density and concluded that density within the immediate area was reduced for 5 years. Little research exists regarding the applicability of localized management in other contexts (e.g., high population density, hunted populations), and without further scientific investigation its applications appear limitless, yet unproven (Campbell et al. 2004).

Particularly in remote areas not accessible to adequate numbers of hunters, localized management may be well-suited for forest management applications. Campbell et al. (2004) assessed the feasibility of using localized management as a management tool within forest regeneration areas in the central Appalachians of West Virginia, on the same study site as our investigation. They reported that female white-tailed deer exhibited high site fidelity and low dispersal, satisfying the *a priori* assumptions of localized management as originally formulated.

Furthermore, they confirmed the conceptual findings of the Adirondack studies and suggested experimental manipulations to test the concept in this setting.

Our objectives in this study were twofold: first we assessed the effectiveness of a microsatellite panel in determining parentage of offspring in a localized group of white-tailed deer; second we used this panel to retrospectively investigate patterns of interrelatedness within a group of deer removed from an 1.1 km^2 area. While known dam-offspring pairs have previously been used to evaluate accuracy of parentage assignment, our study is the first to evaluate the accuracy of this microsatellite panel in the context of a free-ranging, closely associated, likely matrilineal group of white-tailed deer. Secondly, we report on a localized removal in a relatively high-density population where removal efforts focused on a geographic area rather than a predefined group of deer. We believe this more closely simulates the methodology most likely to be useful in contexts including forest management and overabundant deer populations.

Study Area

Our study was conducted on MeadWestvaco's 3,360-ha Wildlife and Ecosystem Research Forest (MWWERF), located in Randolph County, West Virginia (38°42'N, 80°3'W). Established in 1994, the MWWERF facilitates the study of industrial forestry's influences on ecological and ecosystem processes in the central Appalachians. The MWWERF is located within the Unglaciated Allegheny Mountains and Plateau Physiographic province (Smith 1995), which is characterized by steep slopes and narrow valleys. Elevations on the MWWERF range from 700 to 1200 m and forest cover is predominantly an Allegheny-northern hardwood forest type. American beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and black cherry (*Prunus serotina*) are the predominant tree species. Species from the mixed mesophytic forest type including yellow-

poplar (*Liriodendron tulipifera*), northern red oak (*Quercus rubra*), American basswood (*Tilia americana*), and black birch (*B. lenta*) are interspersed throughout much of the site. Rosebay rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) dominate the shrub layer throughout. The highest elevations support communities dominated by red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). As an artifact of high deer herbivory pressure and past forest management activities, understories of hay-scented fern (*Dennstaedtia punctilobula*) dominate throughout.

A detailed investigation of the deer herd on the MWWERF began in 1999. Pre-harvest deer densities and sex ratios during the study were estimated at 12-20 deer/km^2 and 6-18 adult males:100 adult females, respectively (Langdon 2001). Abomasal parasite counts suggest the herd was at or near nutritional carrying capacity (Fischer 1996).

Methods

Experimental Removal

During January and February 2002, we captured deer within a circular 1.1 km^2 area (Fig. 4.1) via modified Clover traps (Clover 1954) baited with whole kernel corn, immobilized them with succinylcholine HCL (SH), and euthanized with a bolt gun. We used SH to enable us to feed the meat to captive carnivores at the West Virginia Division of Natural Resources Captive Animal Facility and Wildlife Park in nearby French Creek, WV. To remove trap-reluctant animals, with the assistance of the West Virginia Disvision of Natural Resources, we employed sharp-shooting to remove as many of the remaining deer within the area as possible. Trapping data, visual observations, and observation of deer tracks in snow were used to confirm the decrease in deer density within the removal area and to determine when to stop the collection effort. We estimated ages of deer via tooth eruption, replacement and wear (Severinghaus 1949).

Genetic Analyses

We collected muscle tissue samples from each deer and fetus and stored them individually in 95% ethanol at 4°C. We isolated DNA using Quiagen® mini-spin columns per manufacturer's recommendations (Dneasy™ Tissue Kit; QUIAGEN Genomics Incorporated, Bothell Wash.), except that tissue lysis was performed overnight. Fragment amplification and separation was performed at the University of Georgia's Integrated Biotechnology Laboratory and followed reaction conditions and a subset of 10 primers (see Table 4.1) described by Anderson et al. (2002). DNA fragments were quantified and analyzed with Genescan® software and alleles were assigned using Genotyper® software (Applied Biosystems, Inc. Foster City, CA) followed by visual inspection and verification (DeYoung et al. 2003). We determined the genotype of each deer on the basis of 10 microsatellite loci (Table 4.1) from the microsatellite panel originally described by Anderson et al. (2002). A full description of the panel and reaction conditions is contained therein.

The software application GENEPOP 3.1 (Raymond and Rousset 1995) was used to perform tests (based on the Markov chain method [1,000 dememorization steps, 100 batches, and 1,000 iterations]) for Hardy-Weinberg equilibrium. We estimated parental exclusion probabilities per locus as well as for all loci combined with CERVUS 2.0 (Marshall et al. 1998). CERVUS employs a maximum likelihood method that requires diploid genetic data and unlinked, autosomal codominant markers. Monte Carlo simulation was used to derive confidence estimates of parental assignment. The program provided estimates of allelic diversity, expected heterozygosity, observed heterozygosity, polymorphic information content (PIC), null allele frequency, and exclusion probabilities (Marshall et al. 1998). Following DeYoung et al. (2003), we compared fetal samples to their known dams to provide an estimate of

the genotyping error rates. In the CERVUS analyses, we considered all deer as potential parents/offspring of all other deer, and considered all fetuses as possible offspring of all females. These comparisons allowed us to evaluate both the accuracy of parentage assignment (via 42 known fetus-dam pairs) and the primary relatedness of deer collected during the experimental removal. The success with which CERVUS assigned fetuses to their correct dam was used to gage other putative dam/offspring pairs. For deer pairs assigned parent/offspring relationships, we also considered animals with the second-highest LOD scores (i.e., the second most likely parent) as likely family members for the purpose of reconstructing probable family groups among the removal deer.

Results

Experimental Removal

From 7 January to 27 February 2002 we collected 39 female and 12 male deer, ranging in age from 0.5–8.5 (mean 3.6$\pm$0.4), and 0.5–3.5 (mean 0.9$\pm$0.3) years of age, respectively. No fetuses were detected in females <1.5 years old; for females $\geq$1.5 years old, a total of 42 fetuses (mean 1.5$\pm$0.1, range 0–3) were present. Tissue samples were unavailable for one male and three females collected during the study. Visual observations, snow track counts, and decrease in trap success confirmed that, although all deer present were not included in the removal, the depopulation effort was largely successful. Based on a concurrent radiotelemetry study on the MWWERF (Laseter2004), 90% of radiocollared inhabitants of the removal area were successfully removed.

Genetic Analysis

Our analysis of the 10 microsatellite loci revealed high polymorphism among the deer we examined; (*k* range: 3–15; x=8.7). The size range and distribution of alleles for each locus were

consistent with that found in previous studies (Anderson et al. 2002, DeYoung et al. 2003). Combined genotyping error rate for the 10 markers was 6.0% (Table 4.1), after the 42 known fetus-dam pairs were compared. The presence of null or undetected alleles was observed in 4 instances at a total of 4 loci. Expected heterozygosity was 0.73 and mean PIC=0.66. Five of the 10 loci deviated (alpha = 0.05) from Hardy-Weinberg Equilibrium (HWE), however minor deviations from HWE are considered acceptable (Marshall et al. 1998, Slate et al. 2000). Of 42 fetuses, 40 were assigned to the correct dam with $\geq$80% confidence; 30 of those were assigned to the correct dam with $\geq$95% confidence. Of the 2 fetuses not assigned to a dam with $\geq$80% confidence, one was nonetheless assigned to the correct dam, whereas one was not. The single incorrect fetus-dam assignment was also responsible for 2 of the 7 mismatching loci found in the entire panel.

Parentage analysis via CERVUS indicated that 33 of the 47 deer sampled were either parents or offspring of at least one other deer sampled. Seven of the 47 deer were closely related (parent and/or offspring) to at least two other deer sampled. Among the 26 adults ($\geq$2 years) sampled, 16 were either parent or offspring of at least one other adult sampled. Animals considered the second most likely parent by CERVUS were considered close family members to reconstruct patterns of inter-relatedness. The results of this reconstruction (Fig. 4.2) indicate that our removal probably included two large family groups, and two or more smaller (or incompletely sampled) groups represented by $\leq$5 deer. Of the 12 bucks included in the removal, parentage analysis suggested 7 were closely related (parent-offspring or full siblings). All of the 7 bucks were $\leq$1.5 years of age and reconstruction suggested that most were closely related to older females, suggesting they were still inhabiting natal range.

Genetic data from a concurrent study of 47 females located outside the removal area (Laseter 2004), but still within the MWWERF were also used to assess relatedness of deer included in the removal. Based on parentage assignment via CERVUS, four removal animals were most closely associated with females located outside the removal area, whereas one removal animal was most closely related to a former inhabitant of the removal area that died two years prior to the removal.

Discussion

We agree that the Anderson et al. (2002) panel has considerable utility in studies of white-tailed deer reproductive success, mating strategies, and socio-spatial dispersion, even within localized groups where individuals are highly related. We assigned correct parentage to 41 of 42 fetuses within a localized group of candidate dams. Estimated parentage exclusion probability was high (Table 4.1), even though many of the individuals were highly related and 5 loci were not in HWE. Previous studies of white-tailed deer microsatellites have attributed HWE deviations to inadvertent sampling of related individuals, even though efforts were made to exclude mother-fawn pairs and other related individuals from the same locality (Anderson et al. 2002). Despite these efforts, 8 of 21 loci in the original microsatellite panel showed deviations from HWE, though the authors concluded that the panel provided enough power to establish parentage in most populations (Anderson et al. 2002).

Our reconstruction of relatedness among removal deer (Fig. 4.2) indicated two relatively large family groups inhabited the 1.1 km^2 removal area, along with several smaller groups. These observations indicate that higher population densities result in matriarchal groups not inhabiting discrete group home ranges as has been observed in other studies (Tierson et al. 1985, Nelson and Mech 1987, Aycrigg and Porter 1997). In addition to female dispersal and

philopatry, population density may prove to be an important determinant in the success of localized management. Regardless, McNulty et al. (1997) hypothesize that localized management will be effective regardless of population density, as long as female dispersal is low. Although plausible, this argument ignores the possibility of widespread encroachment as maturing females establish adjacent but overlapping home ranges differentially at the periphery of a newly created void in the population. Our findings of two large family groups and several smaller (or incompletely sampled) groups included in a 1.1 km^2 area indicates that spatially-based localized management in high density populations can be expected to remove both complete and incomplete social groups. We believe the potential for the incompletely-removed peripheral social groups to colonize newly-created voids is high. Depending on the application of localized management in a given area (forestry, agriculture), persistent zones of low deer density may be difficult to maintain. Where feasible, more traditional approaches aimed at increasing hunter participation and antlerless harvest may still be necessary to control density at larger scales.

Our parentage assignment tests indicated that the majority of the dams were related to at least one other individual included in the removal, consistent with populations exhibiting high philopatry and site fidelity and low dispersal (Campbell et al. 2004, Laseter 2004). The four deer (Figs. 4.1 and 4.2; asterisks) most closely related to non-removal animals may have either been removed during a seasonal movement, or may have been animals that dispersed into the removal area when they were fawns. These four deer were genetically related to deer inhabiting other areas within the MWWERF, but two were >3 km away, while two inhabited home ranges adjacent to the removal area.

Campbell et al. (2004) reported that female deer on this site displayed high site fidelity, that a significant portion of female deer ranges were traditional, and that female deer exhibited low dispersal rates. Deer densities on our site were 3-4 times greater than those observed in the Adirondack studies (McNulty et al. 1997, Langdon 2001), thus there appears to be much more potential for multiple family groups to have overlapping home ranges on our study site. Patterns of inter-relatedness among deer (Fig. 4.2) in our removal area suggest that multiple family groups inhabited the estimated 1.1 km^2 area, and that we may have included a few individuals from adjacent family groups as well.

McNulty et al. (1997) removed 14 animals within a 1.4 km^2 area in the Adirondacks of New York. These animals were members of a predefined, radiomonitored social group selected for removal. As documented for other groups in their study area, members of this group collectively made seasonal migrations between winter yards and summer ranges. McNulty et al. (1997) predict that, in practice, localized management would not require extensive knowledge of sociospatial structure and relatedness of deer. To be a practical management tool, localized management would need to focus on a geographical area, removing all deer in the area (regardless of their relatedness to one another) until none remained. This methodology would be expected to remove $\geq$1 social group, plus peripheral members of adjacent groups. In application, however, McNulty et al. (1997) retrospectively calculated their 1.4 km^2 removal area as based on the composite home range of the targeted social group. In contrast, we focused our removal on a predetermined area because in most management scenarios, biologists will not have detailed social group information available.

In the Adirondack studies, population density at the time of the removal was estimated at 6 deer/km^2, decreasing to an estimated 2 deer/km^2 throughout the following decade, as the result

of a region-wide decrease in deer population (Oyer and Porter 2004). Considering the higher population density on our study area, removal of 52 animals from the 1.1 km^2 area is consistent with population density estimates on our study area being $\geq$4 times that in the Adirondacks. Oyer and Porter (2004) recently reported on the persistence of the removal area created by McNulty et al. (1997). They concluded that the 1.4-km^2 area of lower deer density persisted for approximately 5 years, and that deer subsequently captured within the removal area were descendants of deer not included in the original removal. Furthermore, Oyer and Porter (2004) report that none of the deer within the removal area were likely dispersers from distant areas, based on low incidence of female dispersal. Whether or not that type of localized area of low deer density will persist on the MWWERF removal area currently is the subject of an ongoing investigation. Our data suggest that 2 of 51 deer in our analysis were related to animals >3 km outside the removal area, also consistent with low dispersal rates. At the high population density found on our study site however, there appears to be much potential for the rare dispersers to colonize newly-created voids, simply based on significantly higher numbers of deer surrounding the void.

Management Implications

Our results support the prediction that a localized removal will tend to target groups of closely related females where high philopatry and low female dispersal are observed. As predicted by Campbell et al. (2004), this population may represent one where localized management is promising, however the partial removal of several overlapping groups suggests that recolonization will occur in this context. The specific application of localized management will determine how persistent the zone of low deer density following a localized removal must be to achieve the desired results. The persistent (5-10 year) zone of low deer density predicted

by previous researchers (Porter et al. 1991, McNulty et al. 1997) may not be realistic for higher density populations where human-deer conflicts often occur. Industrial forest applications in the central Appalachians, may however require only 2-3 growing seasons to allow successful regeneration. While the sociobiological attributes in our study population indicate that localized management has promise, it is likely that population density is also a critical factor in the persistence of a void in the deer population created by localized management. The result in a low-density herd in the Adirondacks may not be fully transferable or applicable to a high-density herd in the central Appalachians.

Acknowledgements

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Table 4.1. Locus-specific summary statistics for 10 microsatellite DNA loci amplified for 89 individuals collected during the course of an experimental removal on the MeadWestvaco Ecosystem and Wildlife Research forest in Randolph County, West Virginia, during winter 2002.

Locus	Heterozygosity		HWE P-value [a]	PIC [b]	Exclusion Probability (both parents unknown)	Genotype error rate [c]
	Expected	Observed				
BL25	0.499	0.538	0.1071	0.420	0.499	0.026
BM848	0.879	0.773	0.0249	0.786	0.879	0
Cervid1	0.871	0.831	0.0394	0.853	0.871	0.024
D	0.820	0.742	0.0000	0.793	0.820	0.024
INRA011	0.557	0.539	0.0002	0.504	0.557	0
K	0.585	0.563	0.5407	0.505	0.585	0
N	0.887	0.792	0.0199	0.871	0.887	0.024
O	0.670	0.761	0.2452	0.608	0.670	0.024
OarFCB193	0.881	0.888	0.0200	0.865	0.881	0.048
R	0.397	0.393	0.3979	0.342	0.397	0.06

[a] *P*-value for test of Hardy-Weinberg equilibrium. [b] Polymorphism information content, an index of polymorphism which is not inflated by rare alleles. [c] Genotype error rate based on 42 fetuses where dam and offspring shared no common alleles for a particular locus.

Figure 4.1. Location of an experimental removal of white-tailed deer within an approximately 600m-radius circle on the MeadWestvaco Ecosystem and Wildlife Research forest in Randolph County, West Virginia, during winter 2002. Dots represent locations from which animals were removed via trapping or sharpshooting. Open circles outside of the removal area represent home range activity centers of 47 radiocollared does from a concurrent study (Laseter 2004) which were used as an outgroup for genetic comparison. Lines connecting open circles to dots within the removal area represent highly related (probable parent-offspring or full siblings) pairs of animals. Asterisks indicate home range activity centers for females located outside the removal area who were closely related (probable parents or offspring) to removal animals.

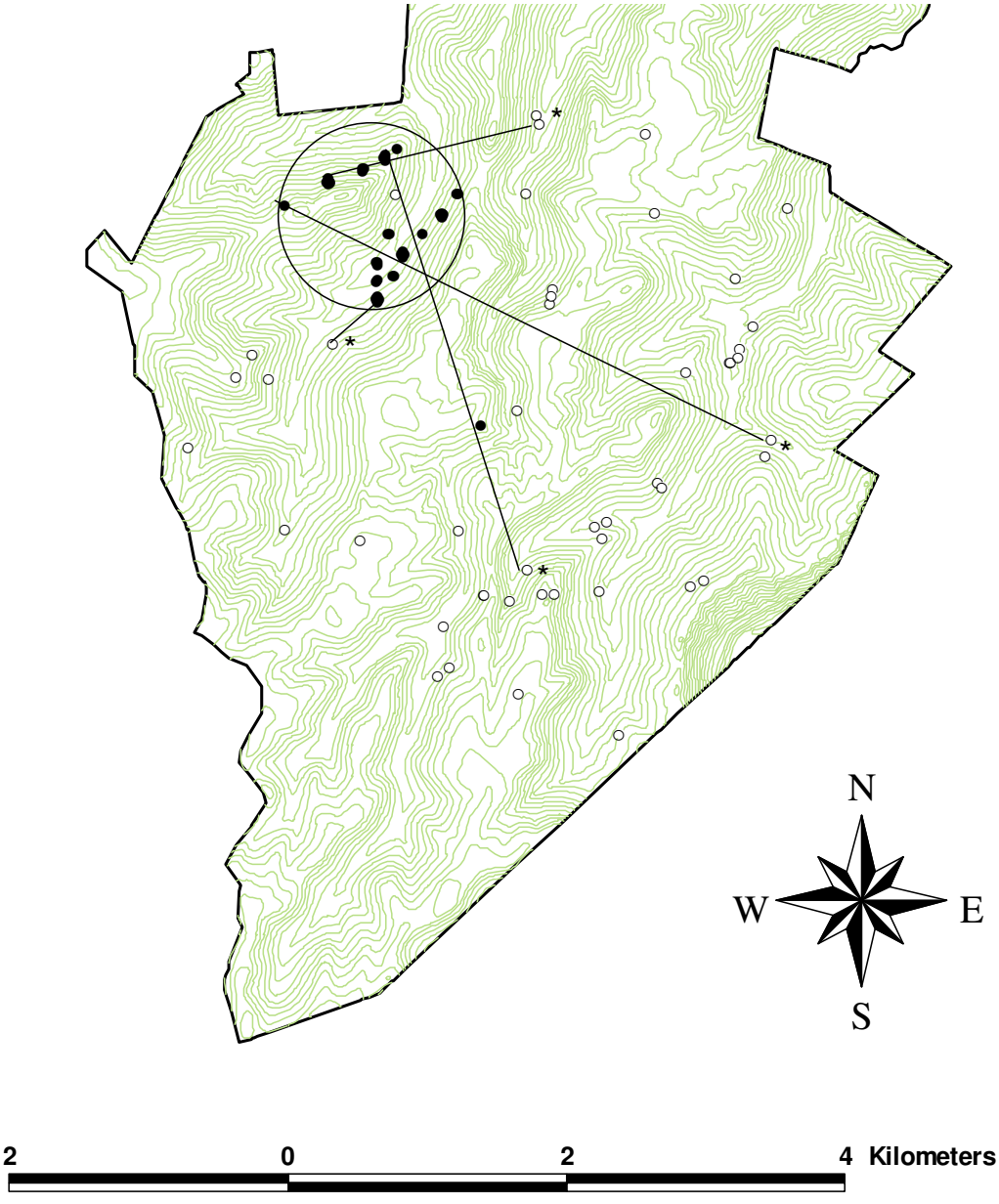
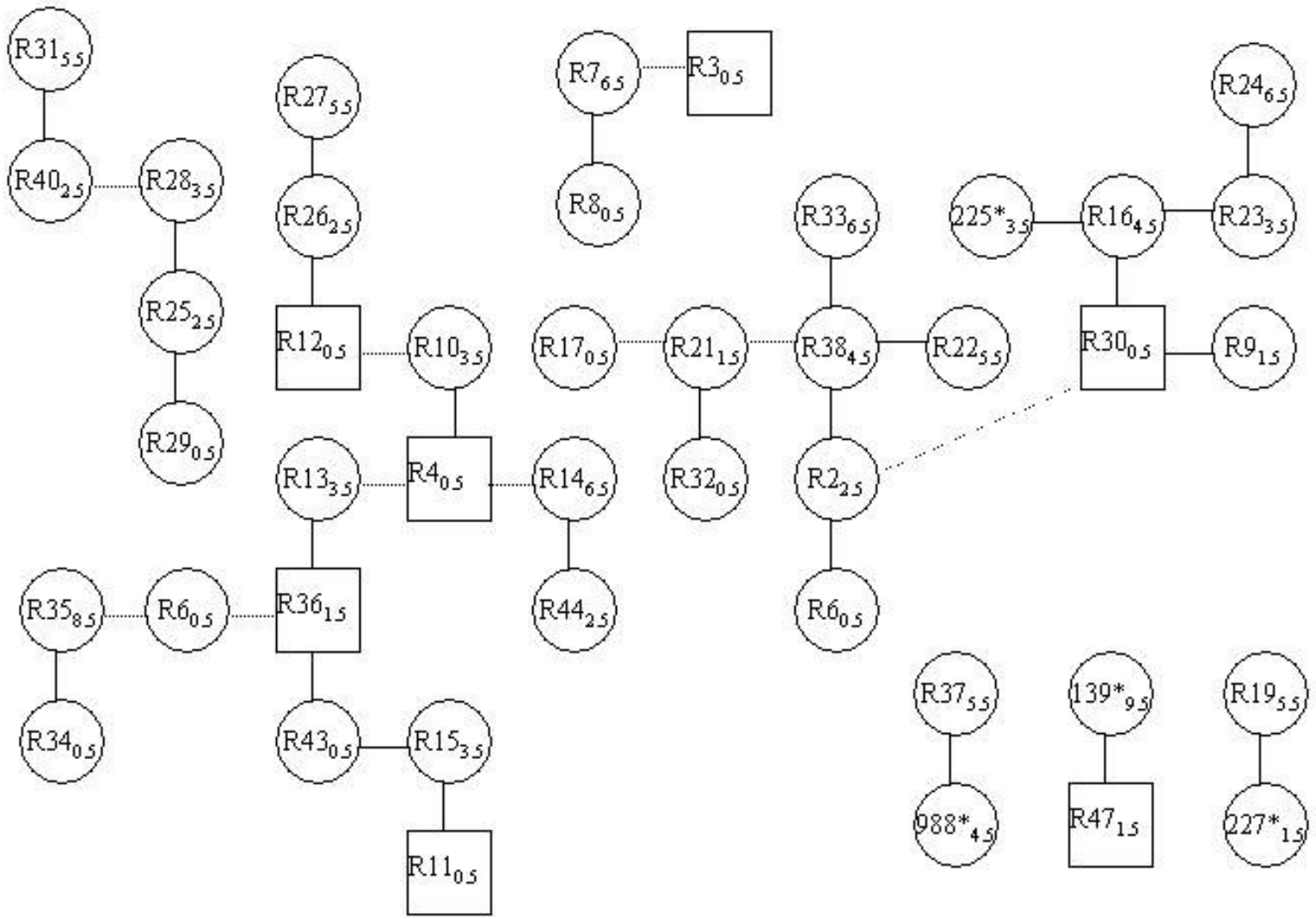

N
W
E
S
2
0
2
4 Kilometers

Figure 4.2. Inferred relationships within four family groups collected during the course of an experimental removal on the MeadWestvaco Ecosystem and Wildlife Research forest in Randolph County, West Virginia, during winter 2002. This figure is not a conventional pedigree, but a representation of the inferred interrelatedness of 36 individual deer. Animals not closely related to at least one other individual (n=12) in the analysis are not represented. Circles represent females, squares represent males. Numbers identify individual animals, subscripts indicate age in years. Solid connectors indicate animals most closely related via highest LOD scores, dashed connectors indicate animals related less closely by second-highest LOD scores. Vertical connectors represent probable parent-offspring bonds, while horizontal connectors represent probable sibship (if solid) or lesser levels of relatedness (if dashed). Asterisks indicate animals located outside the removal area who were closely related (probable parents or offspring) to removal animals.


R31 5 5
R40 2 5
R28 3 5
R25 2 5
R29 0 5
R27 5 5
R26 2 5
R12 0 5
R10 3 5
R13 3 5
R4 0 5
R14 6 5
R35 8 5
R6 0 5
R36 1 5
R34 0 5
R43 0 5
R15 3 5
R11 0 5
R7 6 5
R3 0 5
R8 0 5
R17 0 5
R21 1 5
R32 0 5
R33 6 5
R38 4 5
R22 5 5
R2 2 5
R6 0 5
225* 3 5
R16 4 5
R24 6 5
R23 3 5
R30 0 5
R9 1 5
R37 5 5
988* 4 5
139* 9 5
R47 1 5
R19 5 5
227* 1 5

CHAPTER 5

CONCLUSIONS

Previous investigations of white-tailed deer (*Odocoileus virginianus*) sociobiology have documented the tendency for females to form matrilineal groups. Particularly, some studies (Porter et al. 1991, Aycrigg and Porter 1997) have attempted to generalize sociospatial behaviors across the wide distribution of the species in North America, based on observations of a few populations. White-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest (MWWERF) in West Virginia exhibit sociospatial characteristics consistent with matrilineal social structure, however certain aspects of their spatial dispersion are notably different than those reported in previous studies. This research expands sociospatial concepts developed in the Adirondacks and elsewhere, and demonstrates that population density confounds (or at least obscures) predictable sociospatial relationships among individuals and groups of female white-tailed deer.

Concurrent research on our study area established that females exhibited high philopatry and low dispersal (Campbell et al. 2004) in a relatively high-density population with female-biased sex ratios (Langdon 2001). In these conditions, females appeared to form stable matrilineal groups with considerable home range fidelity, however these groups did not inhabit exclusive geographic areas as observed in previous studies, nor was spatial arrangement of individual females within these groups dependant upon age. Examination of genetic population substructure confirmed not only that individuals distributed themselves nonrandomly across the

landscape of our study area but that genetic structure was present and was largely coincident with spatial groups.

My findings question the universal applicability of behavior-based concepts such as the rose-petal hypothesis and localized management. The importance of site-specific population-level dynamics must be understood before behavior-based management strategies, such as localized management can be effectively implemented. Although my results confirm the existence of spatial and genetic structure consistent with matrilineal groups of white-tailed deer, demographic variation has resulted in important sociospatial differences in my study population. I believe the most important difference in this population and those of previous sociospatial studies is population density. Population density on the MWWERF was 4-5 times higher than that observed in the Adirondacks, where the rose-petal hypothesis was formulated. My findings bring attention to an behavioral attribute that was previously underestimated, that being behavioral plasticity in response to high population density.

My data also suggest that while the patterns of inter-relatedness observed in our study are consistent with matriarchal social structure reported in previous studies, higher population density may affect the composition of deer groups removed in spatially-based localized management efforts. Overall, the rose-petal model of white-tailed deer population expansion applies to my study population, but high population density forces overlap among matriarchal groups and may limit the effectiveness of localized management efforts.

My overall study objectives were to build upon the baseline movement data of Dr. Tyler A. Campbell (Campbell 2003) in order to describe the sociospatial and genetic characteristics of white-tailed deer in the central Appalachians of West Virginia. This work should, in turn, provide the basis for subsequent theoretical and practical sociobiological investigations in the

central Appalachians. A forthcoming dissertation by Bradley F. Miller of the Warnell School of Forest Resources at the University of Georgia will address a test of localized management in the central Appalachians.

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APPENDIX A

NOTES ON GENETIC SAMPLES AND TECHNIQUES USED FOR WHITE-TAILED DEER ON THE MEADWESTVACO WILDLIFE AND ECOSYSTEM RESEARCH FOREST, 1999-2002

The purpose of this appendix is to briefly describe the success (or lack thereof) of various approaches to tissue collection and preservation used in my study. Details of the extraction and amplification procedures, as well as the microsatellite markers used, can be found in chapters 2-4 of this dissertation, as well as the references contained therein.

The present study involved collecting tissue samples from immobilized or dead white-tailed deer for the purposes of DNA extraction and subsequent genotyping. Initially, <1ml of whole blood was collected from each animal and placed directly in approximately 8ml of Longmire solution. Preliminary results from DNA isolation procedures suggested that this procedure did not provide sufficient nuclear DNA for reliable PCR amplification and genotyping of our microsatellite panel. The Longmire solution itself was also suspected to reduce DNA yield and success in PCR amplification. The majority of the blood samples collected in this manner yielded no microsatellite data.

Following these results, I began to collect ear-notch (cutaneous) samples in addition to blood samples for each animal. Ear-notches were preserved in 95% ethanol, allowed to fix at 4C for >24 hours, and stored at room temperature. At the same time blood samples were increased to approximately 2ml whole blood and 6ml Longmire solution. The cutaneous samples yielded much more consistent success in both extracting the DNA and subsequent PCR amplification. The higher concentration blood samples were somewhat more successful than the previous blood samples, but were still not reliable.

The final phase of the present study included the genetic analysis of fetus-dam pairs, and utilized muscle tissue from both dam and fetus. These muscle samples were fixed and stored as previously described for the ear-notch samples. Adult muscle tissue samples yielded acceptable amounts of DNA, but yielded less than fetal samples. Fetal samples yielded less DNA than ear-

notch samples, but were also acceptable and reliable tissues for the purpose of DNA extraction, PCR amplification, and microsatellite genotyping. I concluded that ear-notch samples stored in 95% ethanol, frozen, or stored in some other suitable preservative are the preferred tissue sample when conducting microsatellite analyses on white-tailed deer. Due to the low number of nucleated cells, mammalian blood proved to be the most difficult tissue for our purposes and should be avoided whenever possible.