

GENETIC VARIABILITY AND MOVEMENT ECOLOGY
OF WHITE-TAILED DEER ON
CHICKAMAUGA NATIONAL BATTLEFIELD PARK, GA

by

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

As the human population continues to increase, less land will be available for wildlife habitat. In the future more species will depend on parks and refuges for suitable habitat in a "sea of expanding development" (Cox, 1993). These parks will be responsible not only for conserving wild populations, but also for ensuring genetic variation necessary for evolutionary adaptations (Allendorf and Leary, 1986).

Genetic variation is important for the health and vigor of a population (Lerner, 1954). In small populations, matings between close relatives are likely to occur. This can result in a loss of genetic variation and inbreeding depression [i.e., a reduction in the fitness of the population due to homogenization of genotypes]. Inbreeding increases the likelihood that an individual will be homozygous for deleterious alleles (Wright, 1969). Highly inbred populations tend to have slow growth rates, low productivity, and high mortality (Lacy, 1992). Furthermore, with fewer genotypes in the population, the probability of an individual being "pre-selected" or "pre-adapted" to future events is reduced. This lessens the population's chance of surviving stochastic events (Lerner, 1954; Allendorf and Leary, 1986). Understanding the importance of genetic variation and the implications of its loss is

important for wise management of wild populations as well as captive breeding programs and restocking efforts.

The exact relationship between heterozygosity and fitness is unknown. Heterozygote superiority at the studied loci, or at closely linked loci, gives a fitness advantage to more heterozygous animals (Mitton and Grant, 1984). Higher metabolic efficiency of heterozygotes could be one mechanism by which this advantage is conferred (Chesser et al., 1982; Liskauskas and Ferguson, 1990). Alternatively, linkage disequilibrium between the examined loci and deleterious recessive alleles also results in higher fitness for heterozygotes (Frydenberg, 1963; Dillon and Manzi, 1988). Heterozygote superiority in this case is almost the exact opposite of inbreeding depression.

Despite the incomplete knowledge regarding the mechanism, the relationship between heterozygosity and fitness is widespread. Levels of genetic heterozygosity have been correlated with fitness-related traits in many animal species from invertebrates (Garton, 1984; Borsa et al., 1992) to birds and mammals (Mitton and Grant, 1984; Rorvik et al., 1990; Teska et al., 1990). Studies using either single enzyme polymorphisms or mean multilocus heterozygosity consistently report significant results (Mitton and Grant 1984). However, some studies show an extremely weak correlation or fail to find a relationship at all (Westneat et al., 1990; Whitehurst and Pierce, 1991).

Heterozygosity and Growth Rates.

Positive relationships between fitness-related traits and heterozygosity have been reported. The majority of studies and some of the earliest work correlated heterozygosity and growth rate in marine invertebrates (Singh and Zouros, 1978; Zouros et al., 1980). Growth rates are important indicators of fitness because, in many species, reproductive success can be increased by attaining a larger size earlier. Typically, differential survival of larger individuals also is seen (Weatherly, 1972; Pierce and Mitton, 1980). In the American oyster (Crassostrea virginica), Singh and Zouros (1978) found a positive association between heterozygosity and growth rate when comparing homozygotes and heterozygotes at five polymorphic loci. Zouros et al. (1980) observed similar results in a later study in which they used seven loci and a larger sample size. Koehn and Gaffney (1984) measured heterozygosity at five loci for the blue mussel (Mytilus edulis), and found more heterozygous individuals had higher growth rates. Laboratory studies using the same species failed to find any relationship (Beaumont et al., 1983). However, these researchers did not consider the same allozymes, and the organisms were taken from opposite sides of the Atlantic Ocean. In the deep sea crab (Chaceon quinquedens), the width of the carapace was positively correlated to the multilocus heterozygosity of six enzymes.

This explained 10-15% of the variation in size (Diehl and Biesiot, 1994).

The association of growth rate and heterozygosity is not confined to the invertebrates. Using a naturalized population of brook trout (Salvelinus fontinalis), Liskauskas and Ferguson (1991) reported that weight and the mean multilocus heterozygosity of 12 loci were positively correlated in females but negatively correlated in males. Single locus effects showed the same results. Development rates have been positively correlated to heterozygosity in a strain of rainbow trout (Oncorhynchus mykiss) (Danzmann et al., 1986); however, Beachum and Withler (1985) reported no genotypic associations in pink salmon (O. gorbuscha) in an examination of eight loci. Increased growth rate has been associated with increased heterozygosity in both mosquitofish (Gambusia holbrooki) (Smith and Chesser, 1981) and herring (Clupea harengus L.) (King, 1985), except at the highest levels of heterozygosity.

Pierce and Mitton (1982) demonstrated a positive correlation between growth rate and heterozygosity in four of five natural populations of tiger salamanders (Ambystoma tigrinum) examined. Almost synchronous breeding by adults assured that size differences were caused by differential growth rate and not age. However, repetitions of the experiment later in the season and in subsequent years failed to find any significant associations. Likewise, Whitehurst and Pierce (1991) did not find a relationship

between weight and heterozygosity at three different growth stages in the spotted chorus frog (Pseudacris clarkii). A significant difference in growth rate was found at one locus, but the heterozygotes weighed less than the homozygotes.

In studies of warm-blooded animals, Garten (1976) demonstrated that in male oldfield mice (Peromyscus polionotus), the more heterozygous animals tended to have heavier body weights. Gaines et al. (1978) reported similar results for voles (Microtus ochrogaster). Fleisher et al. (1983) examined house sparrows (Passer domesticus) to determine if a relationship between heterozygosity and growth occurred. They found a positive correlation between body size and heterozygosity at two loci, but only in female birds. Finally, in white-tailed deer (Odocoileus virginianus), fetal growth rate has been correlated to both the fetal and maternal heterozygosity level (Cothran, 1983). Also, more heterozygous does tended to attain a greater overall bodyweight than their less heterozygous counterparts (Chesser and Smith, 1987). However, less heterozygous deer developed to maturity more rapidly than those does with higher heterozygosity levels.

Heterozygosity and Survival Rates

Numerous studies have attempted to link survivorship to heterozygosity. Many investigators report a positive association between heterozygosity and age (Zouros and Foltz, 1987). Age-related changes usually are conducted by

examining percentages of heterozygotes in different age classes. A larger percentage of heterozygotes in the older age classes suggests differential survival of heterozygotes, as long as emigration and immigration are not significant factors. Age-related changes in heterozygosity proportions have been reported in clams (C. virginica) (Zouros et al., 1983), blue mussels (M. edulis) (Diehl and Koehn, 1985), and other invertebrates (Zouros and Foltz, 1987).

Studies on vertebrates tend to confirm these findings. In an Oregon population of western toads (Bufo boreas), a post-winter sample contained a larger percentage of heterozygotes than a pre-winter sample (Samollow and Soule, 1983). Differential mortality of homozygotes was thought to account for this percentage change. Non-winter seasons did not show this change, nor was there a significantly higher proportion of heterozygous adults compared to hatchlings. A study using multilocus heterozygosity in a naturalized brook trout population showed that genetic variation changed among age classes (Liskauskas and Ferguson, 1991). Significant differences were detected between 1 to 2-year-old versus 4-year-old fish. The older fish had more heterozygous loci per individual. However, there were no differences between young-of-the-year and 3 to 4-year-old fish.

There are relatively few studies of survivorship based on marked individuals. Most studies of this type examine single-locus effects to survivorship although many different loci are studied. Redfield (1974) found that in blue grouse

(Dendragapus obscurus), heterozygosity and survivorship were correlated. However, the relationship was only reported in adult birds after a particularly harsh winter. In a study of the Eastern cottontail rabbit (Sylvilagus floridus), Scribner et al. (1983) found both single-locus and multilocus variability to be lower after the winter season. This was attributed to either homozygote superiority or a greater tendency for heterozygotes to disperse in winter months. Pemberton et al. (1988) examined genotypes of juvenile red deer (Cervus elaphus L.) at three loci. Heterozygote superiority was found at two of the three loci but the deer that were homozygous for the third locus tended to have greater survival rates.

Heterozygosity and Fitness Traits

Fitness is defined by differential reproductive success. Any traits that enhance an organism's reproductive success increase its fitness. In brook trout, Liskauskas and Ferguson (1991) found a positive association between female multilocus heterozygosity and the number and size of eggs produced. In addition, treating the loci separately explained more of the variation than combining them.

Chesser and Smith (1987) found that more heterozygous female white-tailed deer tended to produce twins more often than less heterozygous does. In males, antler symmetry and number of points were found to increase with heterozygosity level. Adult body size, testis weight, and kidney fat levels were reported to be correlated with both

heterozygosity and age (Smith et al., 1982). These characteristics are advantageous to males during the breeding season when they compete for mating opportunities (Marchinton and Hirth, 1984).

Behavior is another fitness-related trait that has been associated with heterozygosity. Aggressive behavior and social dominance determine a large proportion of an individual's reproductive success in some species (DeFries and McClearn, 1970). In dark-eyed juncos (Junco hyemalis), an increase in dominance was found with heterozygosity at one metabolic enzyme (Baker and Fox, 1978). Rorvik et al. (1990) found that more heterozygous willow ptarmigans (Lagopus lagopus lagopus) had access to territories more often than less heterozygous birds. However, the birds with an intermediary level of heterozygosity had more mating opportunities. Among mammals, Garten (1976, 1977) found more heterozygous mice (P. polionotus) were more aggressive and engaged in more exploratory behavior than less heterozygous mice. This behavior may be important in food scouting and in acquiring a better knowledge of the terrain for predator avoidance.

Genetic and Telemetric Research in Deer

The white-tailed deer is an excellent species in which to investigate the relationships between individual heterozygosity and fitness parameters. Much is known about the biology and ecology of white-tailed deer (Halls, 1984). Thus, the likelihood of successfully attributing variation

in the data set to a known cause is greater. White-tailed deer are highly heterozygous mammals, especially for a large, vagile species (Selander and Kaufman, 1973; Breshears et al, 1988). Even when examining relatively few loci, there is enough variation in the species to assign heterozygosity levels to individuals. Comparisons can then be made among these levels.

Radio-telemetry research allows the determination of home range size and quality, which may be indicative of fitness. In white-tailed deer, more dominant males have relatively larger home ranges (Green, 1988). Animals whose range is composed of relatively high-quality habitat should have a fitness advantage because of an increased ability to meet their needs. Quality usually is described in terms of preferred vegetation and cover (Cypher and Cypher, 1988). The preferred habitat can change seasonally with phenological patterns of plants (Cypher and Cypher, 1988). Other factors, such as proximity to roads (Lyon, 1983) and adjacent land use patterns also could influence habitat quality.

In summary, the studies described above suggest that careful consideration of genetics is necessary because there are genotypic components to fitness in a variety of organisms. The literature demonstrates a need for further investigation of the relationship between heterozygosity and fitness-related traits. Although the relationship is not always found or very strong, the fact that it is present in

animals ranging from clams to deer indicates that it is a real phenomenon. Elucidating these relationships will permit more knowledgeable conservation decisions. The white-tailed deer, although abundant, could serve as a model for rare or threatened mammals.

Objectives

The objectives of this study were to determine and describe the genetic variation found in the deer population of Chickamauga National Battlefield Park, Georgia and to correlate this variation with fitness indicators as measured by home range size, quality, and other movement parameters. Samples for genetic analysis were collected at the time of deer capture. Mary Ratnaswamy ran the electrophoresis for deer captured through 1992 and I completed the electrophoresis for deer captured in 1993 and 1994. Home range quality was measured by the presence and proportion of specific vegetation types. Home ranges were determined seasonally and sex considerations were included in the analysis. Telemetric data was collected between December 1991 and September 1994, with the first six seasons of home ranges determined by Carolyn Rogers. I hypothesized that the more heterozygous individuals would tend to have larger ranges because of a tendency to be more active or inquisitive. I also predicted that the more genetically variable deer would have a higher proportion of their home range in higher quality habitats.

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CHAPTER II

CORRELATIONS BETWEEN GENETIC VARIATION AND HOME RANGE SIZE
AND QUALITY IN WHITE-TAILED DEER¹

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Genetic variation is important for the health and vigor of a population (Lerner, 1954). Correlations between an individual's heterozygosity level and fitness-related traits are found in many species (reviewed by Zouros and Foltz, 1987). These traits include growth-rate (Danzmann et al., 1986; Garton, 1984; Pierce and Mitton, 1982), survival (Liskauskas and Ferguson, 1991; Pemberton et al., 1988; Redfield, 1974), and behavior (Garten, 1977; Rorvik, 1990). The white-tailed deer (Odocoileus virginianus) is a highly heterozygous species (Breshears et al, 1988), for which fetal growth rate, overall body weight, and antler symmetry and number of points are positively correlated to heterozygosity levels (Cothran, 1983; Chesser and Smith, 1987, Smith et al. 1982).

A limitation in many studies has been the method of tissue collection for electrophoretic analysis. Only a small number of loci are scorable from blood; therefore, studies requiring more loci must use samples from post-mortem animals. As a result, very few genetic studies involve marked animals that are monitored over a relatively long study period (Pemberton et al., 1988; Redfield, 1974; Scribner et al., 1983). A new, sterile, muscle biopsy technique for deer significantly increases the number of loci that can be studied (Ratnaswamy et al., 1993). Tissue samples can be collected pre-mortem, which allows the animal to be monitored subsequently. Then, genetic data can be

correlated to fitness-related parameters while the animal is still alive.

Fitness-related parameters associated with home range size and quality can be measured with radio-telemetry and correlated with an individual's heterozygosity level. Total size of the home range is an indicator of fitness. For male deer, a larger home range increases the number of females he may encounter and thus may increase reproductive success. Also, size of a home range could indicate an animal's tendency to explore (Lunney and Leary, 1989).

An animal whose home range encompasses higher quality habitat will be better able to meet its needs, which will enhance its likelihood of survival and reproductive success (Trivers, 1972). Hardwood forests are important ecologically for deer because they provide both food and shelter (Halls, 1984). Also, hardwood forests typically provide more browsing opportunities than coniferous forests. A deer with a high proportion of its home range contained in this type of forest probably will require less effort to meet its survival needs.

In this study, we examine the genetic variation of the deer herd on Chickamauga Battlefield National Military Park, Georgia and determine individual heterozygosity at eight polymorphic loci. An individual's home range values, determined from radio-telemetry, are correlated with its heterozygosity. We hypothesize that the more heterozygous

animals will have larger home ranges. We also predict that the more heterozygous animals will have higher quality home ranges, as defined by availability of important habitat types.

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MATERIALS AND METHODS

Study Area

Chickamauga Battlefield Park (CBP) is a roughly square area of 2,268 ha (Van Horn, 1981) located in Catoosa and Walker counties of northwestern Georgia. Eleven different habitat types were described by Rogers et al. (1993) and digitized into a Geographical Information System (GIS) base. The Park contains 1,995 ha of forest with 8 ha of cedar glades, which is a rare and threatened plant community. Dominant trees in the overstory include pines (Pinus spp.), oaks (Quercus spp.), and hickories (Carya spp.) The understory also contains oaks and hickories as well as red maples (Acer rubrum), dogwood (Cornus florida), ash (Fraxinus spp.), red cedar (Juniperus virginiana), and elm (Ulmus spp.). The remaining 223 ha is mostly in fields, mowed twice per annum, dominated by fescue (Festuca pratensis) and low hop clover (Trifolium campestre) (Rogers

et al., 1993). CBP receives an annual average of 133.6 cm of precipitation. The mean annual temperature is 15.4°C with an average January and July temperature of 3.7°C and 25.9°C, respectively (Rogers et al., 1993). The elevation ranges from 109-209 m above sea level (Van Horn, 1981).

Chickamauga Battlefield Park is surrounded by urban development (Fort Oglethorpe, GA) to the north, a golf course and suburban developments to the east, and large tracts of primarily agricultural land to the south and west. West Chickamauga Creek flows along the southeastern border of the park (Rogers et al., 1993). CBP is bisected by U.S. Highway 27, which is an important travel route to Chattanooga, Tennessee. This highway is a major source of mortality for the deer, with 75-100 deer-vehicle collisions occurring each year.

Excluding automobiles, which are responsible for 75% of the annual mortality, few other mortality factors exist for the deer (Rogers, 1995). Hunting is not permitted within park boundaries, although poaching does occur. However, deer that range beyond the borders of CBP are subject to bow-hunting pressures during deer season.

The deer herd appears to be healthy. Necropsies performed on all road-killed deer found most of the animals to be in good condition. Furthermore, annual deer herd health collections indicate a relatively healthy population, not overly burdened with disease or parasites. Also, the

lack of a browse line suggests that overpopulation is not a problem (Stromayer, 1995).

Deer Capture and Sample Collections

Deer were captured with the use of drop nets and darting techniques. Nylon drop nets (Ramsey, 1968) were pre-baited with corn prior to capture to acclimate the deer to the net. Darting was accomplished with a Paxarms dart gun (PAXARMS Mesa, Arizona) fired at close range from a pickup truck (Jenkins, 1955).

Between December 1991 and March 1992, 40 deer were captured. Efforts were made to collect deer of both sexes and all age classes (fawn, yearling, adult). The uneven age and sex ratios as well as differential survival made it impossible to maintain equivalent numbers of male and female animals. Another 11 deer were captured in December 1992 to replace animals that had lost their collar or died in the previous year. An additional four deer were darted during Winter 1993. Subsequently, 11 more deer were captured in late summer and late fall of 1993 with the final two deer captured in early Spring of 1994.

Deer were immobilized with an intramuscular injection of a xylazine hydrochloride (Rompun: 1-1.5mg/kg body weight) and ketamine hydrochloride (Ketaset: 10-15mg/kg body weight) mixture (Mech et al., 1985). Capture myopathy was reduced with an intraperitoneal infusion of 1000 meQ of sodium bicarbonate in 0.15% saline (Conner et al., 1987).

After radio-collaring and tissue collection, the deer were roused quickly with an injection of yohimbine hydrochloride (0.1-0.5mg/kg body weight), given both intramuscularly and intravenously (Mech et al., 1985).

Tranquilized deer were given a unique identification number and fitted with Advanced Telemetry Systems, Inc. (ATS Isanti, Minnesota) radio-collars equipped with mortality switches. If the collar did not move for a period of 8 hours, then a mortality signal was transmitted. This allowed for rapid relocation of lost collars or retrieval of the carcass after an animal's death. The collars were then refitted to newly captured deer. Plastic ear tags with an identifying number were placed on each deer for visual identification (Beasom and Burd, 1983).

Captured deer were weighed and aged (Severinghaus 1949). Blood (10 ml) and muscle samples (0.5 g) were taken from most deer. The muscle biopsy procedure was completed as described in Ratnaswamy et al. (1993). Some animals were not completely immobilized, thus making it impossible to obtain blood and/or muscle samples. Blood samples were drawn from the jugular vein into heparinized blood tubes. They were kept on wet ice until refrigerated. Blood was centrifuged within 48 hours and plasma and hemolysate stored separately in cryogenic vials in liquid nitrogen. Muscle samples were kept on wet ice for no longer than 30 min. until transfer to liquid nitrogen was possible. Tissue

samples were kept in liquid nitrogen or in an ultracold freezer until electrophoretic analysis.

Genetic Analysis

Blood and muscle samples were examined using horizontal starch gel electrophoresis (Selander et al., 1971; Manlove et al., 1975). This procedure yielded 18 presumptive loci (Ratnaswamy et al. 1993). Procedures followed Breshears et al. (1988) for all enzymes except adenosine deaminase (Ada) and isocitrate dehydrogenase (Icd-1, Icd-2). Ada was analyzed from muscle on a lithium hydroxide gel and Icd-1,-2 were analyzed from muscle on a Tris-maleate gel. Fumerate hydratase (Fh), mannosephosphate isomerase (Mpi-1), peptidase (Pep-1, Pep-2, Pep-3), creatine kinase (Ck-2, Ck-4), glucokinase (Gk), malic enzyme (Me-1, Me-2), and α -glycerophosphate dehydrogenase (α -Gpd) were scored from muscle tissue. Albumin (Alb), plasma protein B (Ppt-B), and transferrin (Tf) were scored from serum and b-hemoglobin (b-Hb) was scored from hemolysate. An effort was made to standardize scorings between electrophoretic analyses, which were accomplished in 1992 and 1994. The results from each analysis were tested as separate populations to determine if there were any significant scoring differences.

Allele frequencies, single locus heterozygosities, and mean multi-locus heterozygosity were calculated using the Biosys-1 program (Swofford and Selander, 1981). These statistics were calculated by season, using genetic scores

from all living, collared animals. Annual changes in allele frequencies and mean heterozygosity were tested for significance by treating them as separate populations and then calculating Wright's (1978) F-statistics. F_{st} values of individual polymorphic loci were compared using contingency chi-square analysis (Workman and Niswander, 1970). Conformity to Hardy-Weinberg equilibrium was tested using Chi-square analysis with Levene's (1949) correction for small sample sizes. Statistical significance was defined at $P \leq 0.05$. Enzymes were considered polymorphic if the frequency of the most common allele was no larger than 0.95.

Radio-telemetry and Home Range Calculations

A thorough telemetry route with permanent locations for standardized collection was developed on the Park. The location sites were entered onto the GIS map of the Park (Rogers et al., 1993). Telemetry was accomplished with a hand-held, 5-element, directional Yagi antenna and receiver. Triangulation (White and Garrot, 1990) was used to locate the animals. Daily attempts were made to locate each collared deer. If this was not possible, a live signal was taken to check for mortality. Both diurnal and nocturnal movements were monitored to record any shifts in habitat use with time of day. Furthermore, the start of the telemetry route was rotated systematically to ensure that an individual's location was not recorded at a similar time

each day. Visual observations of collared animals were recorded as a location if they were seen during a scheduled telemetry shift.

All locations were converted to X-Y coordinates based on the Universal Transverse Mercator (UTM) system. Coordinates for visual observations were either digitized into GIS using a Calcomp Digitizer 9500 or entered interactively into the GIS map of the Park. Data were sorted into seasonal categories for analysis. Seasons were defined as follows: Winter (16 Dec-15 Mar), Spring (16 Mar-15 Jun), Summer (16 Jun-15 Sep), and Fall (16 Sep-15 Dec). Telemetric data were collected from Winter 1992 through Summer 1994, for a total of 11 seasons. These seasons are based on phenological changes in the plant communities of the park (Rogers, 1995).

Seasonal locations were entered into the computer program HOMERANGE (Ackerman et al., 1988). This program graphically depicted each deer's range using the 95% harmonic mean method. This method eliminates outliers from the analysis. Within each season, an Analysis of Variance (ANOVA) was used to determine if there was any sex effect on home range size. Seasons were kept stratified for all analyses (Beier and McCullough, 1990), which were performed using the SAS statistical package (SAS, 1985). Statistical significance was accepted at $P \leq 0.05$.

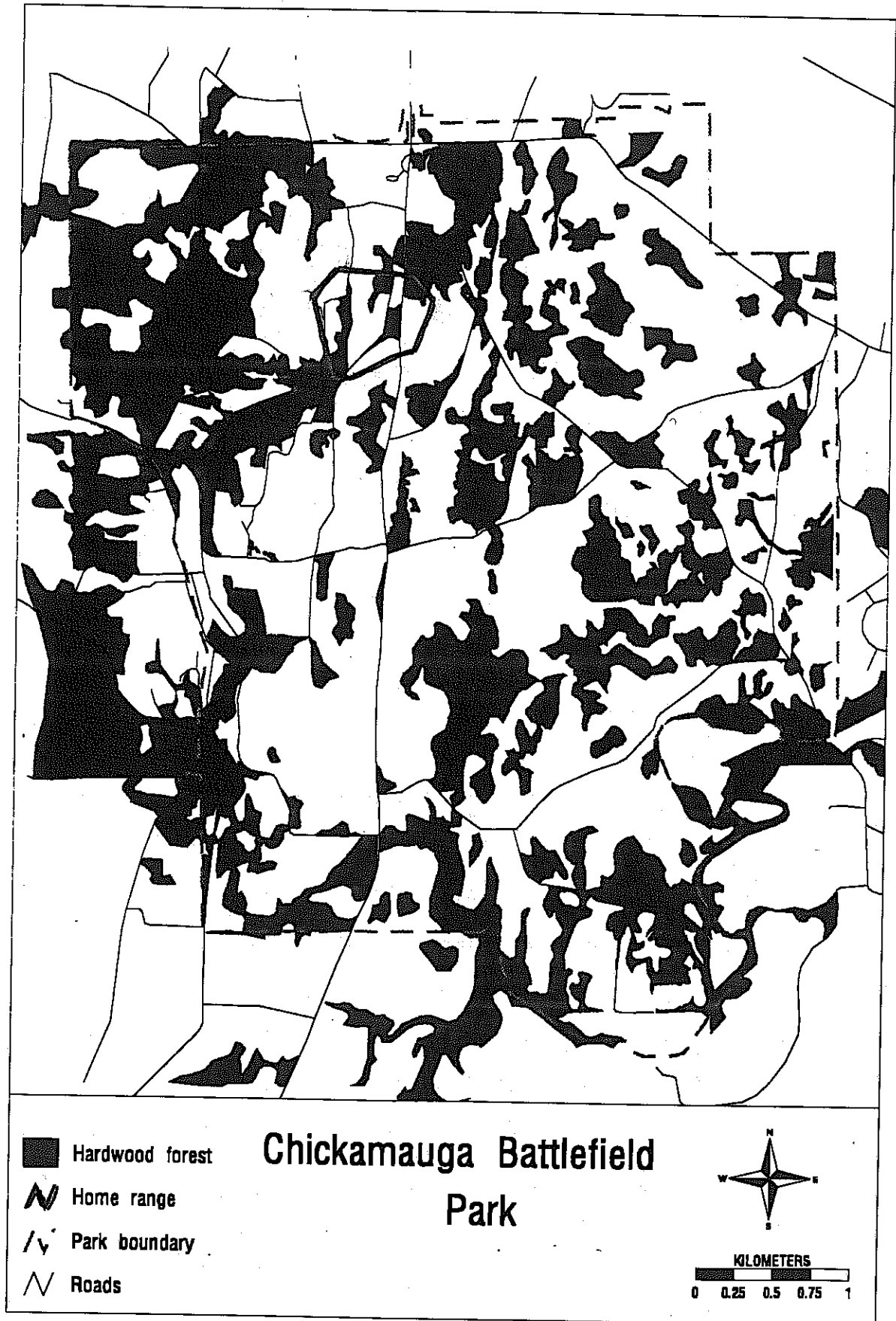
Eleven different habitat types were delineated in the Park (Rogers et al., 1993) and home ranges were overlaid on the GIS map of the Park's habitat types (Rogers et al., 1993). The area in each of the eleven habitat types for each deer in a particular season was calculated (Figure 1). Areas were calculated in m^2 and converted into ha. Then, the proportions of each habitat type were determined.

Statistical Analysis

Seasonal changes in home range size and proportion of habitat types are typical for white-tailed deer (Beier and McCullough, 1990). For this reason, data were kept stratified by season. This eliminated the problem of non-independence among seasons while still keeping adequate sample sizes. We grouped deer into three heterozygosity classes: high, medium, or low based on an individual's number of polymorphic loci. Two-way ANOVAs with sex and heterozygosity class as main effects tested for sex effect, heterozygosity class effect, or sex-by-heterozygosity class interaction. If the sex effect and interaction term were non-significant, then a one-way ANOVA using all deer in that season was performed. All P-values were determined from Type III sum of squares.

In each season, ANOVAs were used to test the effect of heterozygosity class on total home range size. Also, the differences in average proportion of hardwood forest was examined by ANOVAs within each season. Arcsin squareroot

Figure 1. A GIS depiction of an individual deer's home range overlaid on the map of Chickamauga Battlefield Park. Hardwood forests are shown to graphically depict proportion of hardwood forest in a deer's home range.



transformations of the proportion of hardwood forest were used in analysis (Steel and Torrie, 1960).

The predictive power of the heterozygosity class was explored by individual regressions of total home range size and proportion of hardwood forest in the home range versus individual heterozygosity. Regressions were stratified according to sex if the two-way ANOVA for that season showed a significant sex or sex-by-heterozygosity class effect. Individual heterozygosity was calculated as a proportion of total number of polymorphic loci (8). The variance was stabilized by arcsin squareroot transformations of individual heterozygosity prior to regression.

RESULTS

Deer Capture and Sample Collection

A total of 81 deer was captured in the course of the study. Of these, 14 were fitted with ear-tags only and 67 were radio-collared. For four of the 67 collared animals, only blood samples were acquired. For an additional seven animals, only muscle samples were obtained. Furthermore, all seven polymorphic loci were not scorable in four deer, although blood and muscle samples were present. Only those animals that had a score for all loci studied were included in the analysis. This limited the total number of deer studied to 52 animals over the three-year period, with a maximum of 24 deer in any particular season.

Genetics

Six loci (Mpi-1, Pep-1, Ada, Me-1, aGpd-2, and bHb) were polymorphic at the 0.95 level. Tf was polymorphic at the 0.95 level in 1992 and at the 0.99 level in 1993. Pep-1 was dropped from the analysis due to scoring problems. Two additional loci were polymorphic at the 0.99 level (Pep-3 and Ck-2). Both bHb and Tf were obtained from blood samples. All others were scored from muscle samples. The mean heterozygosity per locus and mean number of alleles per locus did not differ significantly between years. The contingency Chi-square analysis showed that allele frequencies of a-Gpd differed significantly between years ($P < 0.04$). Allele frequencies, single-locus heterozygosities, and mean multi-locus heterozygosity were calculated for each year (Table 1). The mean number of alleles per locus was 1.71 ($SE = 0.22$) in 1992 and 1.47 ($SE = 0.19$) in 1993. Allele frequencies did not deviate significantly from Hardy-Weinberg expected values.

For each polymorphic locus, a heterozygous score was given a value of one and a homozygous score was given a value of zero. These values were summed for individual deer. The minimum sum was zero and the maximum was four. Deer were assigned to heterozygosity classes based on their individual sums. A score of 0 or 1 was considered "low", a score of 2 was "medium", and a score of 3 or 4 was "high".

Table 1. A comparison of allele frequencies (freq), single-locus heterozygosity (h), and mean multi-locus heterozygosity (H) for the polymorphic loci found in the deer herd at Chickamauga Battlefield Park

Locus ^a	Allele	1992		1993	
		Freq	h ^b	Freq	h ^b
Mpi-1	122	0.281	0.438	0.238	0.286
	100	0.719		0.762	
Pep-3	105	0.016	0.031	0.000	0.000
	100	0.984		0.000	
Ada	107	0.047	0.125	0.071	0.143
	100	0.938		0.929	
	95	0.016		0.000	
Ck-2	117	0.984	0.032	0.000	0.000
	100	0.016		0.000	
Me-1	128	0.188	0.375	0.225	0.250
	100	0.813		0.775	
aGpd-2	112	0.344	0.313	0.425	0.450
	100	0.656		0.575	
Tf	100	0.983	0.033	0.929	0.143
	92	0.017		0.071	
bHB	120	0.081	0.710	0.095	0.667
	110	0.097		0.095	
	100	0.419		0.405	
	95	0.403		0.405	
H ^{bc}			0.121		0.114
SE			0.051		0.043

^aLocus abbreviations in text

^bHeterozygosities are direct count estimates

^cMean multilocus heterozygosity includes 10 monomorphic loci in addition to polymorphic loci listed here

These classes were used as classification variables in subsequent ANOVAs.

Home Range Calculations and Statistical Analysis

Home range estimates were based on a minimum of 16 and a maximum of 64 locations. Within a season, the number of locations per animal was roughly equivalent but among seasons this number varied greatly. Data collected in Winter 1994 (15 Dec 93 - 16 Mar 94) were not analyzed because of the small number ($n=7$) of locations for each animal.

Data from the ANOVAs are summarized by years for 1991-1992 (Table 2), 1992-1993 (Table 3), and 1994 (Table 4). The two-way ANOVAs showed sex to have a significant effect on home range size in Spring 1992 ($P<0.015$), Spring 1993 ($P<0.001$), Fall 1993 ($P<0.053$), and Summer 1994 ($P<0.017$). In Spring 1993, the sex-by-heterozygosity interaction was significant ($P<0.008$; Table 3). This also was the only season in which the difference in home range size was significant among heterozygosity classes ($P<0.008$). In this season, as well as in Summer 1994, the average home range of males in the "medium" class was significantly larger than in the "high" class. No males occurred in the "low" class in either season. In Spring 1992 and Fall 1993, the males in the "high" class had the largest average home range (Tables 2 and 3). When female home ranges were examined for these seasons, the "medium" class had the largest average home

Table 2. Average home range size and proportion of hardwood habitat with corresponding sample sizes for male and female white-tailed deer by heterozygosity class in each season (1991-1992)

Season	Sex	Heterozygosity Class	Number of deer	Home Range size (ha)		Proportion in hardwoods	
				Mean	SE	Mean	SE
Winter	Male (Pooled) ^a	Low	3 (7)	193.84	42.65	0.1685	0.0359
		Medium	4			0.2832	0.0375
		High	(8) 4 (7)	166.34 245.69	30.83 29.54	0.3368	0.0045
	Female	Low	4			0.3512	0.0342
		Medium	4			0.3507	0.0319
		High	3			0.3876	0.0381
Spring	Male	Low	4	677.81	238.42	0.2012	0.0303
		Medium	4	516.67	139.60	0.3151	0.0152
		High	3	729.34	147.86	0.3460	0.0182
	Female	Low	7	279.45	51.33	0.3642	0.0191
		Medium	4	359.54	153.42	0.3534	0.0113
		High	3	315.30	54.51	0.3552	0.0176
Summer	Male (Pooled)	Low	4 (10)	165.60	22.53	0.1965	0.0510
		Medium	4			0.2640	0.0190
		High	(8) 4 (6)	139.93 225.20	25.49 60.19	0.2876	0.0569
	Female	Low	6			0.3212	0.0162
		Medium	4			0.3546	0.0260
		High	2			0.2783	0.0092
Fall	Pooled	Low	8	172.87	29.49	0.3550	0.0263
		Medium	9	283.32	77.59	0.3326	0.0181
		High	7	230.97	55.15	0.3453	0.0353

^aIf sex and sex-by-heterozygosity class interaction were non-significant then data for males and females were pooled together.

Table 3. Average home range size and proportion of hardwood habitat with corresponding sample sizes for male and female white-tailed deer by heterozygosity class in each season (1992-1993)

Season	Sex	Heterozygosity Class	Number of deer	Home Range size (ha)		Proportion in hardwoods	
				Mean	SE	Mean	SE
Winter	Pooled ^a	Low	8	166.39	36.19	0.3583	0.0318
		Medium	6	187.45	58.57	0.3723	0.0329
		High	8	167.80	27.84	0.3454	0.0389
Spring	Male (Pooled)	Low	0 (7)			0.3271	0.0314
		Medium	1 (6)	679.38			
		High	5 (7)	243.28	77.60	0.3689	0.0283
	Female	Low	7	93.99	10.22		
		Medium	5	147.44	27.61		
Summer	Pooled	High	2	123.36	22.27	0.3111	0.0363
		Low	8	74.67	11.84	0.3397	0.0478
		Medium	7	81.37	28.68	0.3370	0.0535
Fall	Male (Pooled)	High	6	86.80	18.67	0.2356	0.0554
		Low	1 (8)	122.29		0.2899	0.0442
		Medium	2 (8)	322.96	209.85		
		High	3 (4)	472.02	237.24	0.3340	0.0373
		Low	7	108.13	12.88	0.2222	0.0543
Female	Female	Medium	6	80.33	21.28		
		High	1	80.79			

^aIf sex and sex-by-heterozygosity class interaction were non-significant then data for males and females were pooled together.

Table 4. Average home range size and proportion of hardwood habitat with corresponding sample sizes for male and female white-tailed deer by heterozygosity class in each season (1994)

Season	Sex	Heterozygosity Class	Number of deer	Home Range size (ha)		Proportion in hardwoods	
				Mean	SE	Mean	SE
Spring	Pooled ^a	Low	6	106.34	35.62	0.3172	0.2702
		Medium	10	113.44	30.81	0.3612	0.0486
		High	4	169.27	24.25	0.2898	0.0423
Summer	Male (Pooled)	Low	0 (8)			0.3111	0.0328
		Medium	2 (8)	300.35	221.01		
		High	2 (3)	175.31	139.59	0.3271	0.0793
	Female	Low	8	76.99	16.92	0.1980	0.0097
		Medium	6	35.54	9.63		
		High	1	19.06			

^aIf sex and sex-by-heterozygosity class interaction were non-significant then data for males and females were pooled together.

range in Spring 1992 and Spring 1993, whereas the "low" class had the largest average home range in Fall 1993 and Summer 1994 (Tables 3 and 4).

When the sex and sex-by-heterozygosity interaction term were non-significant, the stratification by sex was removed and a one-way ANOVA was performed. In Fall 1992 and Winter 1993, the "medium" class deer had the largest average home range, although it was not significantly larger (Tables 2 and 3). In all other seasonal periods, the average home range of deer in the "high" class was larger than in the other classes, although it again was not significant. In Fall 1992, Winter 1993, Summer 1993, and Spring 1994, the deer of the "low" classification had the smallest average home ranges (Tables 2, 3, and 4).

The quality of home range (i.e., proportion in hardwood forest) was tested by two-way ANOVAs, with sex and heterozygosity class as the classification variables. Sex was a significant main effect (Table 2) in Winter 1992 ($P < 0.05$), Spring 1992 ($P < 0.02$), and Summer 1992 ($P < 0.025$). For both males and females in Winter 1992, the "high" class had a larger proportion of hardwoods than the other two classes. This held true for Spring 1992 and Summer 1992 for males but not for females, where the "low" class had the highest proportion in Spring 1992 and the "medium" class in Summer 1992 (Table 2). The proportion of hardwood forest also was significantly related to heterozygosity class

($P < 0.05$) in Winter 1992 (Table 2). In Summer 1993, the heterozygosity class and sex effects were nearly significant ($P < 0.09$ and $P < 0.08$ respectively; Table 3). The sex-by-heterozygosity class interaction was not significant in any season. Data from male and female animals were grouped together in the remainder of the seasons. Heterozygosity class was not a significant classification variable in any of these seasons ($P < 0.37$ - $P < 0.85$).

Based on findings of the ANOVAs, the regression equations for total home range size as a function of individual heterozygosity were stratified by sex in Spring 1992, Spring 1993, Fall 1993, and Summer 1994. In all other seasons, data from both male and females were pooled. This created 14 separate regression analyses (Table 5). No significant relationships were found. The most significant regression was a negative correlation found in Summer 1994 ($P < 0.10$; Table 5). In nine seasons, the relationship was positive with the more heterozygous deer having the larger home ranges. The slope of the regression line was negative in the five other seasons examined.

A highly significant ($P < 0.01$) positive relationship between proportion of hardwood forest and individual heterozygosity was discovered in Winter 1992 for male deer (Table 6). The only other relationship that was nearly significant was in Summer 1993 ($P < 0.15$). This was a negative relationship, as were most of the regression

Table 5. Linear regressions of total home range size (TOT) on arcsin (individual heterozygosity) (HET) for white-tailed deer on Chickamauga Battleground Park

Season ^a	Regression equation	N	R ²	F
Winter 92	TOT = 176.35 + 44.43 (HET)	22	0.012	0.237
Spring 92 (M)	TOT = 677.05 - 82.39 (HET)	11	0.004	0.032
Spring 92 (F)	TOT = 302.74 + 15.72 (HET)	11	0.001	0.005
Summer 92	TOT = 140.49 + 61.24 (HET)	23	0.012	0.447
Fall 92	TOT = 189.94 + 76.42 (HET)	23	0.108	0.240
Winter 93	TOT = 164.29 + 15.01 (HET)	21	0.001	0.018
Spring 93 (M)	TOT = 646.09 - 448.2 (HET)	6	0.044	0.182
Spring 93 (F)	TOT = 72.43 + 95.53 (HET)	14	0.133	1.848
Summer 93	TOT = 68.75 + 23.34 (HET)	20	0.013	0.251
Fall 93 (M)	TOT = 3.15 + 569.8 (HET)	6	0.083	0.360
Fall 93 (F)	TOT = 130.13 - 78.18 (HET)	14	0.098	1.302
Spring 94	TOT = 44.83 + 146.8 (HET)	19	0.092	1.815
Summer 94 (M)	TOT = 780.38 - 804.2 (HET)	4	0.252	0.673
Summer 94 (F)	TOT = 98.04 - 96.90 (HET)	15	0.204	3.325 ^b

^aIf two-way ANOVAs showed a significant sex effect, separate regressions were run for males (M) and females (F)

^bP<0.10

Table 6. Linear regressions of arcsin(hardwood/total home range size) (HRD) on arcsin(individual heterozygosity) (HET) for white-tailed deer on Chickamauga Battlefield Park

Season ^a	Regression equation	N	R ²	F
Winter 92 (M)	HRD = 0.2465 + 0.495 (HET)	11	0.550	10.984 ^b
Winter 92 (F)	HRD = 0.6253 + 0.037 (HET)	11	0.025	0.231
Spring 92 (M)	HRD = 0.5617 + 0.063 (HET)	11	0.093	0.921
Spring 92 (F)	HRD = 0.6510 - 0.019 (HET)	14	0.014	0.165
Summer 92 (M)	HRD = 0.4050 + 0.200 (HET)	12	0.152	1.790
Summer 92 (F)	HRD = 0.6302 - 0.050 (HET)	12	0.046	0.480
Fall 92	HRD = 0.6647 - 0.074 (HET)	24	0.051	1.184
Winter 93	HRD = 0.6950 - 0.104 (HET)	22	0.045	0.937
Spring 93	HRD = 0.6893 - 0.138 (HET)	20	0.098	1.948
Summer 93	HRD = 0.6871 - 0.224 (HET)	21	0.114	2.449 ^c
Fall 93	HRD = 0.6031 - 0.081 (HET)	20	0.010	0.187
Spring 94	HRD = 0.6082 + 0.007 (HET)	20	0.001	0.001
Summer 94	HRD = 0.6161 - 0.102 (HET)	19	0.015	0.259

^aIf two-way ANOVAs showed a significant sex effect, separate regressions were run for males (M) and females (F)

^bP<0.01

^cP<0.15

slopes. Positive relationships were seen for males in Winter 1992, Spring 1992, and Summer 1992 and for the sexes combined in Spring 1994. All other regressions had negative correlations.

DISCUSSION

We found heterozygosity level to be a significant factor in determining home range characteristics only in a small number of seasonal periods tested. Heterozygosity level was important for total home range size in Spring 1993. Deer in the "medium" class had significantly larger ranges than those in other classes. This is consistent with the observation by Rorvik et al. (1990) that willow ptarmigans (Lagopus lagopus) of medium heterozygosity held the largest territories.

The sex-by-heterozygosity class interaction term was highly significant in this same season. This indicates that males and females respond differently to heterozygosity effects. This may be due to differences in home range requirements of females as fawns are born (Marchinton and Hirth, 1984).

The large variance in home range sizes also makes it difficult to detect any differences among the heterozygosity classes. In other studies with white-tailed deer, heterozygosity effects accounted for no more than 20-25% of the variance in characters that were much less variable than home range size (Cothran, 1983; Chesser and Smith, 1987;

Smith et al., 1982). Larger sample sizes might reduce this problem.

We had thought that a larger home range might indicate an individual's tendency to explore. Garten (1977) found that more heterozygous mice (Peromyscus polionotus) tended to engage in more exploratory behavior. Lunney and Leary (1989) found that exploratory behavior caused male white-footed dunnarts (Smithopsis leucopus) to have larger home ranges. The use of the 95% harmonic mean method to determine home ranges in this study might have obscured exploratory behavior. This method excludes outliers from the analysis and may have hidden the true extent of exploration for some deer.

Home range quality was measured by the proportion of hardwoods in the total home range. Only in the first winter season (Winter 1992), was hardwood habitat significantly related to heterozygosity. The deer in the "high" class used the largest proportion of hardwoods and those deer in the "low" class used the smallest proportions in their home range. Prior to this season, the mast production had been poor (Rogers, 1995). Availability of mast is extremely important as a source of high-quality food before winter begins (Halls, 1984). The poor mast crop in the Fall of 1991 may be related to the increased proportion of hardwood habitat in the more heterozygous animals the following winter. As food became scarce, the animals with more

available mast might have a fitness advantage (i.e., greater energy). Heterozygosity effects are thought to be more pronounced under more stressful conditions (Mitton and Grant, 1984; Teska et al., 1989; Mulvey et al., 1994). This could explain why heterozygosity effects were seen in the first winter of the study but not in the second, when the mast production was significantly higher (Rogers, 1995). Also, the heterozygosity effects were stronger for males. This would be predicted because males are under more nutritional stress than females in the winter due to mating activities.

Heterozygosity was not a good predictor of home range characteristics. Regression lines of total home range size were non-significant in all seasons. In Summer 1994, there was a nearly significant negative relation of individual heterozygosity and total home range size. The proportion of hardwoods was positively related to individual heterozygosity in Winter 1992 for males. Again, this may be because of the poor mast crop in Fall 1991. In all other seasons, it was not a significant variable for predicting proportion of hardwood forest in a deer's home range.

A curvilinear relationship between heterozygosity and fitness-related traits has been seen in previous studies (Rorvik et al. 1990). However, in preliminary analyses for this study, adding the square of the heterozygosities to the regression equations lessened the correlations. Deer of

medium levels of heterozygosity do not appear to have significantly larger home ranges or a greater proportion of hardwood forest in their home ranges.

A significant relationship between heterozygosity and a fitness-related trait, such as home range parameters, would not be surprising. Fetal growth rate in white-tailed deer corresponded to both the fetal and maternal heterozygosity level (Cothran et al., 1983). The overall body weight of does was greater for more heterozygous individuals (Chesser and Smith, 1987). These does also tended to produce twins more often. In males, antler symmetry and number of points was found to increase with heterozygosity level. Adult body size, testes weight, and kidney fat levels were correlated with both heterozygosity and age (Smith et al., 1982).

Home range parameters, such as size and quality, are related to many intrinsic and extrinsic factors. Sex, age, and population density all contribute to the determination of an individual's home range. This study failed to find conclusive evidence that home range size or proportion of preferred habitat is affected by multilocus heterozygosity. However, heterozygosity effects are believed to be more pronounced under stressful conditions (Mitton and Grant, 1984; Teska et al., 1989). The deer on CBP are not under strong population pressures. There are adequate food and space resources for the population. Herd health collections and kidney fat indices show that the herd is in good

condition. The lack of a browse line also suggests that food availability is not a limiting factor (Stromayer, 1995). Perhaps a deer herd with strong population pressures or other severe environmental stresses would show a more significant correlation between heterozygosity and home range size and quality. Alternatively, there could be no relation between home range parameters and heterozygosity. The other factors determining home range characteristics may limit the heterozygosity effect to an insignificant amount.

The largest obstacle in this study was our small sample sizes. The expense and difficulty of capturing and radio-collaring deer, coupled with the time constraints of radio-tracking, limited our sample sizes. The skewed sex ratio and differential mortality also contributed to the unequal numbers of male and female animals in the different heterozygosity classes among seasons. Future research employing a smaller species (e.g. oldfield mice, P. polionotus) could increase sample sizes because the time and cost of capturing a relatively large number of animals would be less. Experimental manipulation of habitats also might be possible if the animals had smaller home ranges than deer. This would allow a controlled test of the correlations between heterozygosity and home range characteristics.

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CHAPTER III
CONCLUSIONS AND RECOMMENDATIONS

I attempted to correlate heterozygosity at seven polymorphic loci with home range characteristics. The sterile muscle biopsy technique provided six additional loci to those previously obtainable from blood samples of live deer. This allowed home range data to be gathered after the genetic samples were collected. Both ANOVAs and regressions were conducted to determine the effect of individual heterozygosity on home range size and proportion of hardwood habitat (i.e., habitat quality). I hypothesized that more heterozygous deer would have larger home ranges and a greater proportion of their home range in hardwood forest, an ecologically important habitat type. However, for most seasons, heterozygosity was neither an important classification variable nor was it a significant predictor of home range parameters. The regression equations resulted in non-significant negative and positive correlations. In fact, the majority of the regression lines had positive slopes for total home range size and there were equivalent numbers of positive and negative slopes for the proportion of hardwood habitat. This supports the prediction that the more heterozygous animals would have larger home ranges but fails to support the prediction that their ranges contain a greater proportion of hardwood forests.

One explanation may be that heterozygosity effects are more evident under stressful conditions. The most significant correlations were found in the Winter of 1992. This winter was preceded by a poor mast crop. This could be

a rare season in which the deer herd was food limited. In general, the deer herd at Chickamauga Battlefield Park is not under severe population pressures. However, CBP is planning to re-route Highway 27. This will lower the number of deer-vehicle collisions substantially and may result in an increase in the deer population. Also, suburban encroachment is reducing the habitat suitable for deer. Therefore, genetic influences may only get stronger in the future. The managers at the Park should consider studying how the genetic structure of the herd changes when the environmental conditions change. This could lead to a better understanding of the importance of the genetic response to habitat variation.