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Review

Genetic heterogeneity of white-tailed deer: management lessons from a long-term study

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Abstract

Genetic data from a long-term (16-year) study of white-tailed deer (*Odocoileus virginianus*) on the U.S. Department of Energy's Savannah River Site (SRS) were examined to evaluate spatial and temporal genetic heterogeneity in this species. Based on our analyses of the long-term data set, three major findings emerged, all of which have important implications for management of white-tailed deer: (1) There exists significant spatial genetic heterogeneity in white-tailed deer based on analyses of allozyme frequencies and mtDNA haplotypes. This heterogeneity exists on a much smaller spatial scale than would be expected for such a large and potentially mobile species as *O. virginianus*. (2) The genetic structure of white-tailed deer at SRS is temporally dynamic and significant heterogeneity exists within demographic units such as age and sex classes. (3) Levels of genetic variation, as measured by multilocus heterozygosity, are frequently correlated to characteristics that are important determinants of ecological function in white-tailed deer populations. These findings are evaluated in the context of a general management model for *O. virginianus* that is also applicable to other wildlife species.

Key words: *Odocoileus virginianus*, allozymes, mtDNA, spatio-temporal heterogeneity, demographic heterogeneity

Introduction

For most of this century, population geneticists and evolutionary biologists have assumed that populations consist of a large number of randomly breeding individuals (panmixia). This view made it easier to mathematically describe the behavior of populations and resulted in a relatively static concept of their genetic characteristics. Little effort was expended in linking genetic and demographic changes in populations. Wildlife biologists considered changes in population numbers, quality of individuals within them, and other demographic parameters as being due to environmental effects, and genetic differences were often not considered at all. Despite this, the environmental or habitat model, which became the almost exclusive population dynamics paradigm in wildlife biology, was very successful in explaining population differences.

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The term "genetics" was not even mentioned in most wildlife management texts during the first two thirds of this century. Technological advances in the 1950s and 1960s made it much easier to describe character variation among individuals and to determine the genetic basis of this variation. There was a virtual explosion in the number of studies that provided estimates of genetic variation in natural vertebrate populations (SMITH et al. 1982, 1994). As a result of these studies, it became clear that the model of a large panmictic population was not correct for most terrestrial and freshwater vertebrates (e.g. SMITH et al. 1978; AVISE 1994). However, most of the data, especially for mammals, were from small relatively short lived forms (e.g. KREBS et al. 1973). Data from the white-tailed deer summarized here support the view that genetic heterogeneity over short distances may be common even in large, vagile vertebrates.

Temporal genetic heterogeneity over short time predicts the need for further refinement of habitat management models used in wildlife management. Characteristics of concern to natural resource management, including conservation, need to be thought of as being due to the influences of Environment (E; Habitat) + Genetics (G; Genotype) + Environment-Genetic Interactions (E*G). A holistic perspective would dictate that the enviromnent-genetic interactions would be at least as important in determining the characteristics of wildlife species as the main effects of genotype and environment. Studies that document differential population responses to similar environmental changes may indicate the importance of environment-genetic interaction and/or differences in the genetic composition of the reference populations. This interpretation stresses the importance of genetic factors in formulating management programs for both game and nongame species.

Genetics is most likely to be important if management units have different genetic characteristics from each other and/or they show temporal variations in their genetic characteristics. Our primary objective is to examine existing genetic evidence to see how common spatial and temporal heterogeneity is in white-tailed deer (*Odocoileus virginianus*, Zimmermann). Our purpose is to review the literature on the genetics of the white-tailed deer, present the results of some new analyses of data from a long-term study of this species, and to propose a new perspective on the important conceptual issues.

Sampling considerations

Management decisions based upon data collected from public hunts need to be viewed with caution. Such data must be examined to determine if inferences can be expanded beyond the limits of the available data in time and/or space. Basically this requires that animals are collected randomly with respect to variables of interest such as sex, age, antler morphology, genotype, etc. Deer collected on the Savannah River Site (SRS) in the southeastern United States, because of the limited public access and the details of the hunting methods used, can generally be considered to represent a random sample of individuals from the herd for most variables of interest (NOVAK et al. 1991). NOVAK et al. (1991) found no hunter selectivity based upon sex but some selectivity based upon age (older deer being preferentially selected) thus slightly biasing the distribution of ages upwards. Thus age-related genetic changes may be harder to detect than genetic changes related to sexual differences.

Spatial heterogeneity

Many genetic studies have shown that white-tailed deer populations are subdivided spatially. The effect is most noticeable in analyses that encompass large geographic areas (CRONIN 1989; ELLSWORTH 1994 a, b; HILLESTAD 1984; KENNEDY et al. 1987). In these studies F_{ST} (or a similar statistic that estimates the proportion of variance among populations) for both diploid (allozymes) and haploid (mitochondrial DNA

[mtDNA]) genetic markers is large, indicating strong differentiation between local populations.

On a small geographic scale, it is possible that spatial subdivision would not exist for a large, potentially mobile mammal, such as the white-tailed deer. However, a number of studies reject this notion. Spatial differentiation of populations for allozyme frequencies was readily apparent in white-tailed deer from the Adirondack Mountains of New York (Mathews and Porter 1993), northeastern Minnesota (Cronin et al. 1991), and on an even smaller scale, the SRS, South Carolina (Manlove et al. 1976; Ramsey et al. 1979), and Cumberland Island, Georgia (Rowland 1989). When studied, mtDNA markers usually, but not always show greater differentiation than those representing the nuclear genome. For example, Cronin et al. (1991) found the F_{ST} value for mtDNA to be 9 times greater than the F_{ST} for allozymes in mule deer from Montana but found no significant difference between mtDNA and allozyme-derived F_{ST} values for white-tailed deer from Minnesota.

Generally, genetic differentiation of populations is attributed to reduced gene flow, historic events and/or genetic drift (Cronin et al. 1991; Ellsworth et al. 1994 a, b; Leberg et al. 1994). In white-tailed deer, gene flow is influenced strongly by the species' mating system, females being philopatric and males doing the majority of movement among breeding groups (Nelson and Mech 1987). The effect of extirpation in the late 1800s and subsequent restocking have had a profound effect on the spatial pattern of genetic differentiation of white-tailed deer populations over most of their range. However, in

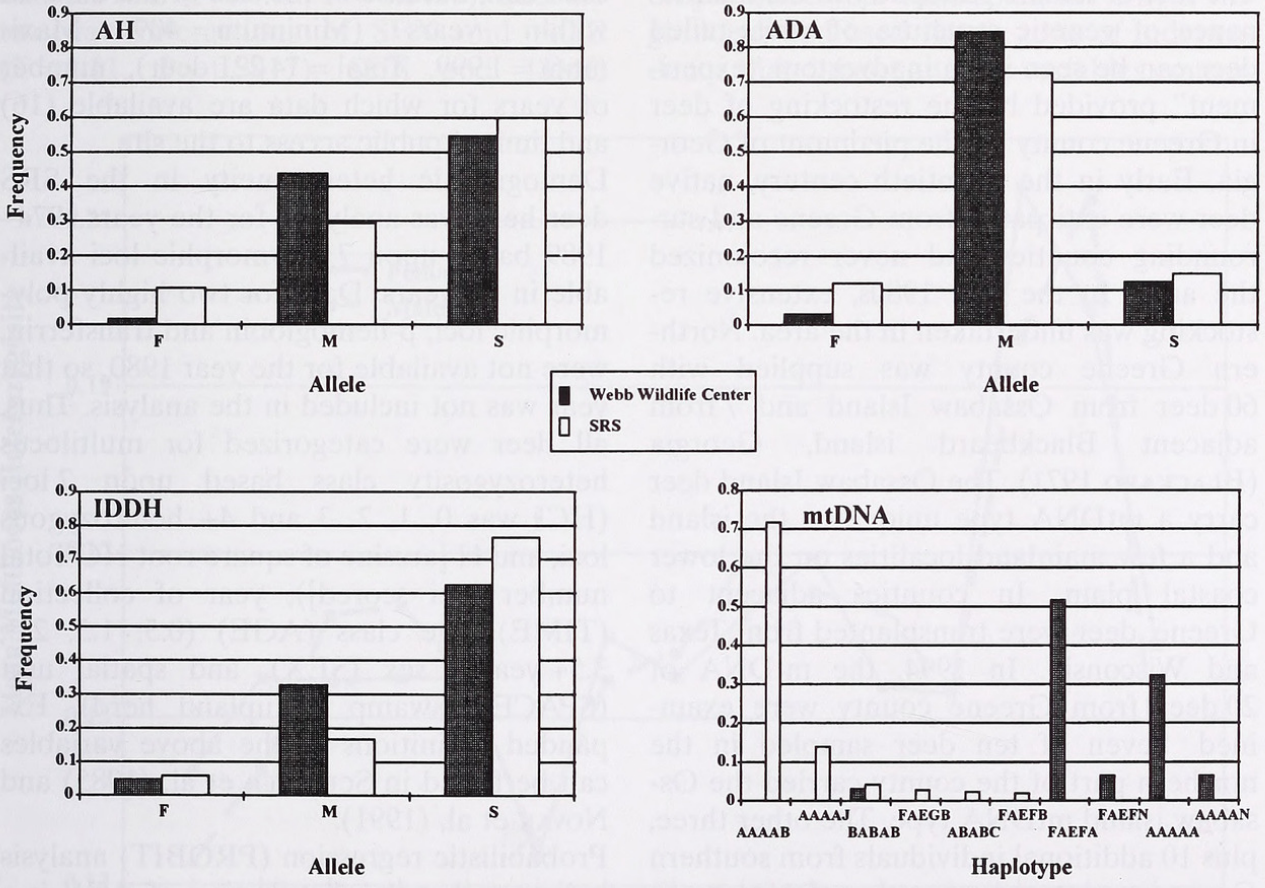

Fig. 1. Comparison of haploid (mtDNA) and diploid (allozyme) genetic markers for white-tailed deer populations collected in 1992 from the Savannah River Site (SRS; $N_{mtDNA} = 215$, $N_{allozym} = 737$) and Webb Wildlife Center (WEBB, $N_{mtDNA} = 31$, $n_{allozym} = 32$). The populations are separated by approximately 100 km. Shown are aconitate hydratase (AH), adenosine deaminase (ADA), and L-iditol dehydrogenase (IDDH) (also known as sorbitol dehydrogenase [SORDH]), the three most variable of the 13 loci sampled. Designations for alleles refer to relative mobility in electrophoretic starch gels. Only haplotypes and alleles with frequencies > 0.01 are shown.

the coastal plain of South Carolina and Georgia, native herds were not hunted to extinction and restocking was minimal. Recent analyses of deer from SRS and Webb Wildlife Center, located 100 km apart on the coastal plain of South Carolina, document significant spatial heterogeneity in both nuclear and mtDNA genomes. Deer sampled from SRS and Webb center display markedly different genetic profiles for nuclear and mitochondrial genes (Fig. 1). This and other studies (KENNEDY et al. 1987) indicate that for allozymes all alleles at a locus are present in most samples, although shifts in frequencies are often observed. In contrast, mtDNA types, which are haploid and maternally inherited, are much more localized. Sometimes, sampling locations separated by only 20 km share no mtDNA types. Female white-tailed deer thus may be extremely philopatric (PURDUE et al. 2000). The role of female philopatry in the maintenance of genetic structure of white-tailed deer can be seen in an inadvertent "experiment" provided by the restocking of deer in Greene county on the piedmont of Georgia. Early in the twentieth century, native deer were extirpated from Greene and surrounding counties and never recolonized the area. In the late 1980s, extensive restocking was undertaken in the area. Northern Greene county was supplied with 60 deer from Ossabaw Island and 7 from adjacent Blackbeard island, Georgia (BLACKARD 1971). The Ossabaw Island deer carry a mtDNA type unique to the island and a few mainland localities on the lower coastal plain. In counties adjacent to Greene, deer were transplanted from Texas and Wisconsin. In 1994, the mtDNA of 20 deer from Greene county were examined. Seven of ten deer sampled in the northern part of the county carried the Ossabaw island mtDNA type. The other three, plus 10 additional individuals from southern Greene county, displayed mtDNA types characteristic of deer from the Midwestern United States. After 40 years and 10–20 generations, female deer from Ossabaw Island have apparently dispersed little beyond their release site. These results reinforce the idea that white-tailed deer are genetically subdivided on a finer geographic scale than is apparent based upon their body size and vagility.

Demographic heterogeneity

Management decisions are usually made for a herd or larger grouping of individuals. However, smaller subsets of individuals (age or sex classes) may be progressing along separate evolutionary trajectories subject to differing ecological challenges. These demographic groups may exhibit different spatial or temporal patterns for both individuals and genotypes. Thus, genetic variability must be analyzed with respect to demographic classes of age and/or sex within a spatio-temporal context. The SRS deer herd provides a unique opportunity to analyze such data because of the size of the data set within years (Minimum = 409, Maximum = 1 999, Total = 14 221 deer), number of years for which data are available (16) and limited public access to the site.

Demographic heterogeneity in the SRS deer herd was analyzed for the years 1974–1989 based upon 7 polymorphic loci available in all years. Data for two highly polymorphic loci, β-hemoglobin and transferrin, were not available for the year 1980, so that year was not included in the analysis. Thus, all deer were categorized for multilocus heterozygosity class based upon 7 loci (HCI was 0, 1, 2, 3 and 4+ heterozygous loci, and H [arcsine of square root HC/Total number loci scored]), year of collection (TIME), age class (AGE) (0.5, 1.5, 2.5, 3.5+ years), sex (SEX), and spatial unit (SPACE) (swamp or upland herd). Expanded definitions of the above variables can be found in SCRIBNER et al. (1985) and NOVAK et al. (1991).

Probabilistic regression (PROBIT) analysis indicates that the distribution of AGE is a function of both TIME and SPACE ($\chi^2 = 61.65$, $P < 0.0001$ and $\chi^2 = 13.09$, $P = 0.0003$, respectively). However, the distribution of SEX is a function of TIME but not SPACE ($\chi^2 = 48.24$, $P < 0.0001$ and

$\chi^2 = 0.69$, $P = 0.4075$, respectively). Thus, analyses of genetic heterogeneity in relation to AGE and SEX must be performed with the appropriate spatial and temporal variables in the analysis.

Probabilistic regression using a Gompertz distribution for HC (GOMPIT) analysis indicates that there are significant SPACE ($\chi^2 = 7.32$, $P = 0.0068$) and TIME ($\chi^2 = 101.64$, $P < 0.0001$) effects, a marginal AGE ($\chi^2 = 6.59$, $P = 0.0863$) effect and no SEX ($\chi^2 = 0.02$, $P = 0.8989$) effect. Unfortunately, interactions among dependent variables cannot be analyzed using a probabilistic regression approach to account for TIME and/or SPACE heterogeneity of SEX and AGE. Therefore, an ANOVA was performed with H as the dependent variables and the main effect of SEX ($F = 0.53$, $P = 0.4676$), AGE ($F = 0.82$, $P = 0.4799$), TIME ($F = 3.84$, $P < 0.0001$), and SPACE ($F = 4.19$, $P = 0.0406$), and the two-way interactions of SEX and AGE ($F = 1.11$, $P = 0.3417$), SEX and TIME ($F = 1.87$, $P = 0.0242$), AGE and TIME ($F = 1.17$, $P = 0.2066$), AGE and SPACE ($F = 0.34$, $P = 0.7930$), and TIME and SPACE ($F = 1.64$, $P = 0.0621$). No higher order interactions were significant, and were therefore not included in the model. The significant interaction of SEX and TIME is due to differenees in H between males and females in different years (Fig. 2). There is no consistent sexual bias in H, 6 years show no significant difference, 5 years show a male bias for higher H, and 4 years show a female bias (Fig. 2).

Previous analysis for the effects of age, sex, year and spatial location on single locus heterozygosity (h) for β-hemoglobin by Chesser et al. (1982) revealed slightly different results. Sex was not found to be an important variable although it is unclear whether a sex by year interaction was tested. This analysis was performed over only a three year time span, for only a single locus and used simple tests of independence that did not analyze variables concur-

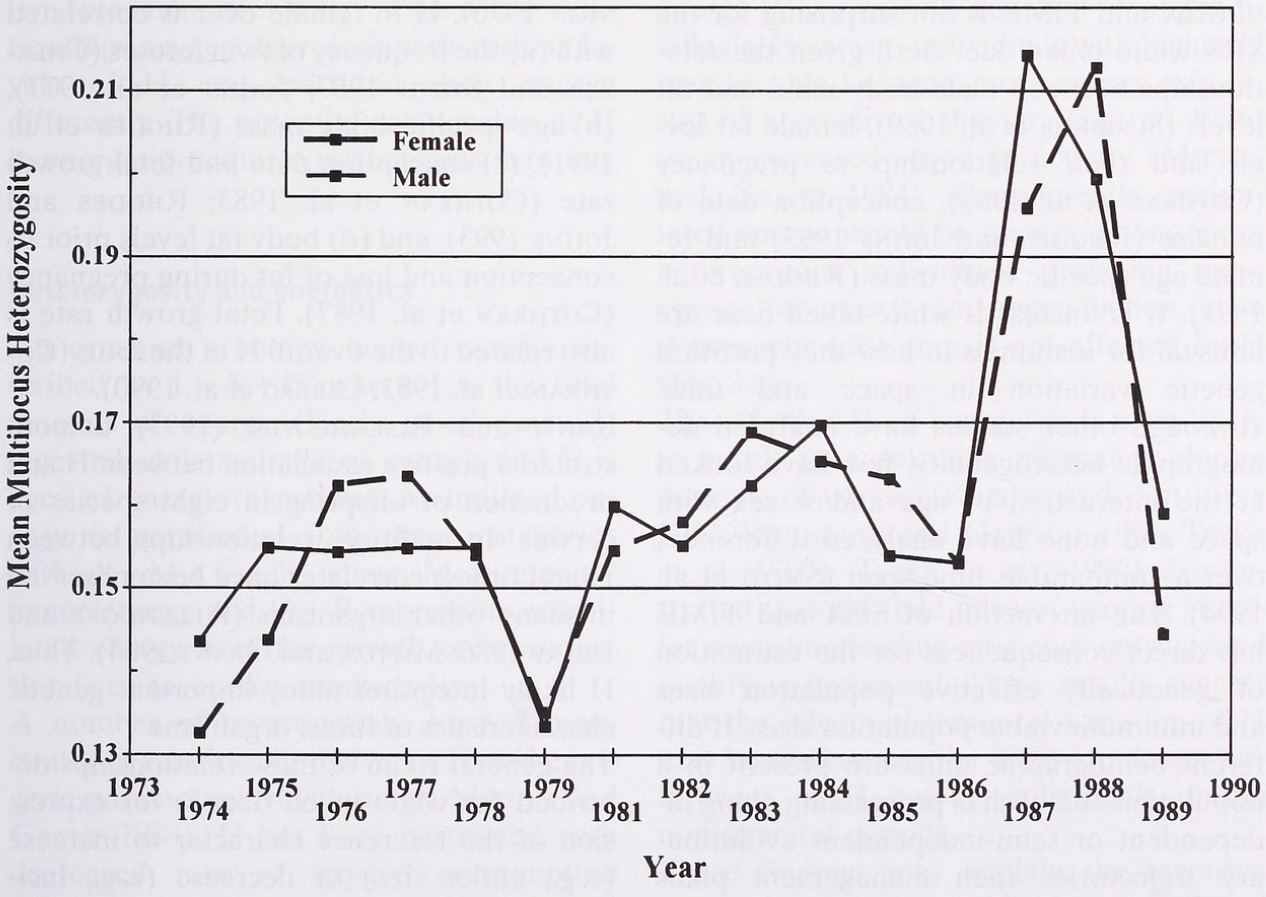

Fig. 2. Multilocus heterozygosity values for male and female deer for the years 1974 through 1989. The year 1980 is not included as indicated in the text.

rently. As indicated by the analyses performed here, there is a much larger range of variation in all variables when analyzed over a longer time span. In addition, longer time series are more likely to include periods of environmental stress. Thus, results based upon data that are limited in time, space or number of loci should be viewed with caution. Differences in results can also be seen in the studies of SMITH et al. (1990) where a significant spatial effect was seen and SCRIBNER et al. (1985) where a significant effect of space was not seen. The first study included data from a longer time series (13 years) than the second (6 years) but both estimated H using the same seven loci used here.

The above analyses illustrate the need to examine demographic effects on genetic heterogeneity in light of spatial and temporal variation of both demographic and genetic variables. Management decisions based upon only the main effect, SEX, would not be the same as those based upon the interaction of SEX and TIME. The interaction of SEX and TIME is not surprising for the SRS white-tailed deer herd given the relationships between male body mass and fat levels (SCRIBNER et al. 1989), female fat levels and their relationship to pregnancy (COTHRAN et al. 1987), conception date of females (RHODES and JOHNS 1993) and female age specific body mass (RHODES et al. 1991). It is unclear if white-tailed deer are unusual for mammals in how they partition genetic variation in space and time. Although other studies have analyzed demographic heterogeneity, few have looked at the interaction of age and/or sex with space and none have analyzed differences over a comparable time span (SMITH et al. 1994). The interaction of SEX and TIME has direct consequences for the estimation of genetically effective population sizes and minimum viable population sizes. If different demographic units are present in a population and each is progressing along independent or semi-independent evolutionary trajectories then management plans need to encompass this heterogeneity. Management decisions must be based upon information gathered to assess the additional ecological and genetic dynamics that such population substructuring introduces.

Fitness correlates and energetics

Fitness correlates

A fitness correlate may be defined as a phenotypic characteristic in which the degree of expression is related to the survival and/or reproductive success (fitness) of an individual. Numerous relationships between multilocus heterozygosity (H) and fitness correlates have been demonstrated in a long-term study of white-tailed deer on the SRS (reviewed by RHODES and SMITH 1992). Within age classes of male deer, H is related to (a) body mass and fat levels (SCRIBNER et al. 1989), (b) antler size (SCRIBNER et al. 1989), (c) antler symmetry and Boone and Crocket scores (SMITH et al. 1991), (d) frequency of spike antlers (SCRIBNER et al. 1984), and (e) testicle size in fawns (URBSTON 1976). H in female deer is correlated with (a) the frequency of twin fetuses (CHESSER and SMITH 1987; JOHNS et al. 1977), (b) age-specific body mass (RHODES et al. 1991), (c) conception date and fetal growth rate (COTHRAN et al. 1983; RHODES and JOHNS 1993), and (d) body fat levels prior to conception and loss of fat during pregnancy (COTHRAN et al. 1987). Fetal growth rate is also related to the overall H of the fetus (COTHRAN et al. 1983; LEBERG et al. 1990).

SMITH and RISENHOOVER (1993) demonstrated a positive association between H and production of offspring in eight species of cervids. In addition, relationships between H and fitness correlates have been observed in many other organisms (ALLENDORF and LEARY 1986; MITTON and GRANT 1984). Thus, H likely integrates many important genetic characteristics of forest organisms.

The general trend of these relationships described for white-tailed deer is for expression of the reference character to increase (e.g., antler size) or decrease (e.g., incidence of spiked antlers) with increasing number of heterozygous loci. However, the

functional relationship varies depending on both the specific character and the age of the deer. In addition, there is evidence to suggest that expression of a reference character may decrease slightly at high H levels compared to that of intermediate levels (e. g., CHESSER and SMITH 1987) although this may be an artifact of small sample size at older age classes.

In most cases, H explains only a small percentage of the variability in characteristics. For example, H is responsible for only 10–15% of the variability in main beam length and diameter of antlers, number of antler points, and incidence of spiked antlers (SCRIBNER and SMITH 1990). Therefore, factors such as age, body condition, habitat, and resource quality, as well as their interaction with H, must be considered when explaining the expression of fitness-related characteristics in individual deer.

Although H may only account for a small amount of the variability in characters, deer with high H generally grow faster, have higher body fat levels and higher reproductive rates than deer with low H. These relationships suggest that deer with various levels of H may partition their energy differently. The potential relationship of H to energetics requires further consideration.

Heterozygosity and energetics

An organism's energy budget can be described by $I = A + E$, where I is the total amount of energy (Kcal $*$ g body mass^{-1}) ingested, A is assimilated energy, and E is egested energy (egestion). Assimilated energy is partitioned into three categories with $A = M + G + R$ where M is maintenance energy and G + R represents assimilated energy used for growth or reproduction (i. e., secondary productivity).

A number of investigations have demonstrated a relationship between H and energetic parameters (reviewed by MITTON and GRANT 1984). H has been correlated with decreased rate of oxygen consumption (KOEHN and SHUMWAY 1982; MITTON and KOEHN 1985; MITTON et al. 1986) and a lower rate of protein turnover (HAWKINS et al. 1986). These findings suggest differences in maintenance metabolism among individuals with varying levels of H.

We hypothesize that increased energetic efficiency could explain the effects of H on fitness-related characteristics in white-tailed deer. Hypothetical energy budgets for an organism with varying H are depicted in Fig. 3. In both homozygous and heterozygous individuals, a portion of assimilated energy must be utilized for maintenance metabolism (M) which includes energy used for normal activity. The remaining energy can be used for secondary productivity (G + R). However, in the more heterozygous individual, increased energetic efficiency as a result of higher H could reduce the amount of assimilated energy required for maintenance metabolism (M). A slight decrease in the amount of energy needed for maintenance could permit heterozygous individuals to partition much more energy for growth and reproduction (G + R, Fig. 3 a).

The above hypothesis assumes that ingested energy (I) is relatively constant among individuals. However, individuals with higher H may be able to ingest more energy as a result of aggressive behavior (GARTEN 1976) or an increased scope of activity (MITTON and GRANT 1984). Consequently, assimilated energy would be greater among more heterozygous individuals, providing more energy for growth and reproduction, even if energetic efficiency is not affected by H (Fig. 3 b).

The effect of H on energetics is most likely to result in a selective advantage during periods of stress (KOEHN and SHUMWAY 1982; RODHOUSE and GAFFNEY 1984; TESKA et al. 1990). TESKA et al. (1990) demonstrated that old-field mice of varying H differ regarding feeding efficiency only as food quality is decreased. These results suggest that the effects of temporal variation of H may be to decrease the ability to detect differences in H among individuals during non-stressful periods.

These findings may explain the inconsistency of some relationships between H and fitness correlates observed in white-tailed

deer. For example, a relationship between H and the frequency of twin fetuses was observed among does from the SRS during the 1970s (CHESSER and SMITH 1987; JOHNS et al. 1977) whereas no such relationship was found during the 1980s (RHODES et al. 1991). Future investigations concerned with documenting H effects in white-tailed deer

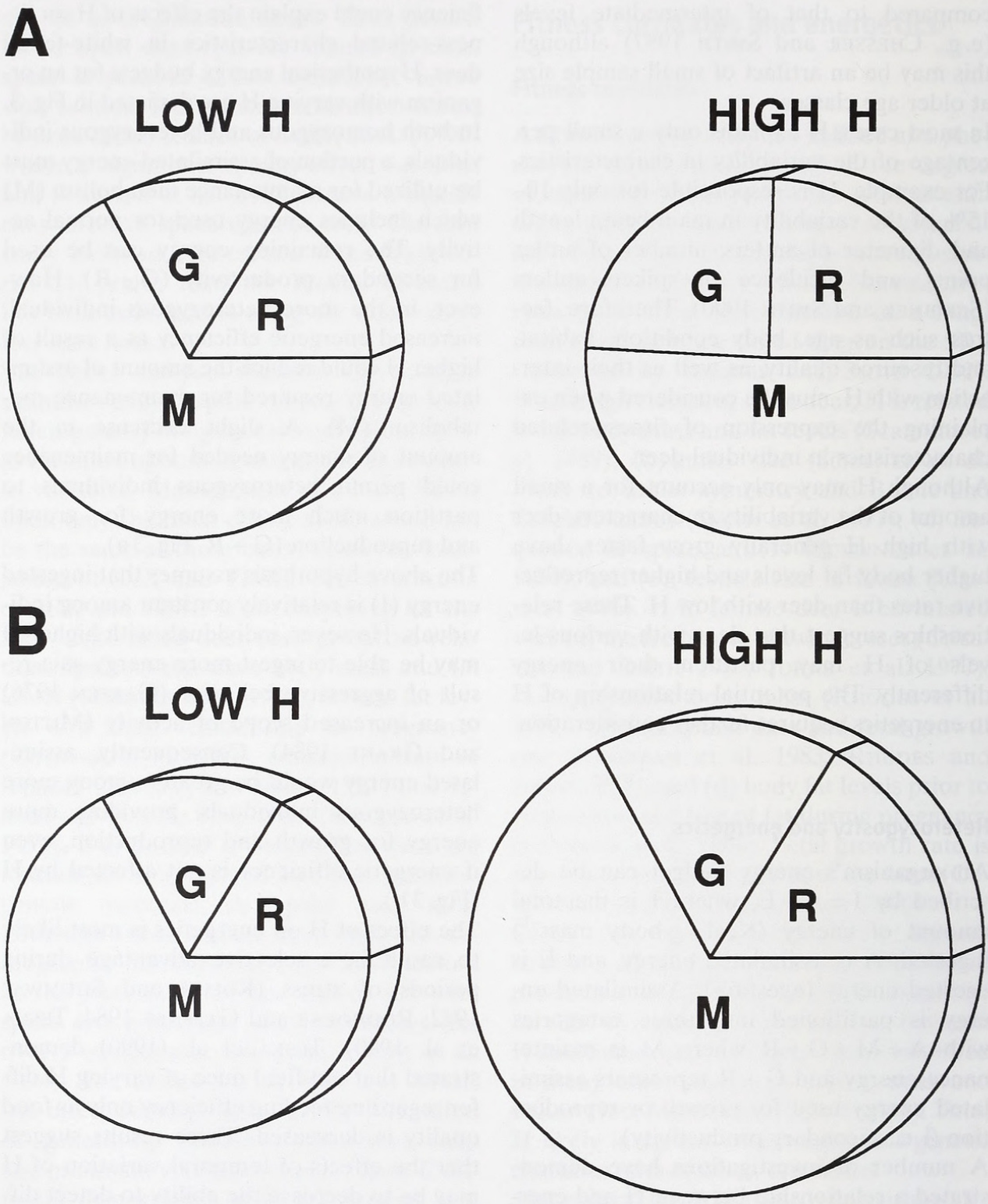

Fig. 3. Hypothetical energy budgets for an organism with relatively low and high levels of heterozygosity (H). High H may increase the amount of energy available for growth (G) and reproduction (R) by: (A) Reducing the percentage of assimilated energy needed for maintenance (M) via effects on metabolic efficiency or: (B) Increasing the amount of assimilated energy via effects on foraging and ingestion. The size of each circle is related to the amount of ingested energy.

should take into account spatial and temporal variation in environmental quality as well as in H.

The influence of H on energetics is related to individual fitness and quality of individuals in a population. Genetic variability could be especially important in allowing forest organisms to persist with increasing levels of anthropogenic and non-anthropogenic stress. Understanding the role of genetic variation has important implications for both conservation and management practices of forest wildlife species.

General management model

Genetic analyses of white-tailed deer populations, as well as other animal populations, have provided insights about their functioning that need to be incorporated in future management plans (Smith et al. 1976). The results of these analyses are especially important to the formulation of management plans. They are as follows: 1) animal populations, especially white-tailed deer, show genetic heterogeneity over relatively short distances and among demographic units within populations, 2) white-tailed deer populations, and probably those of other species, are generally dynamic over short time periods, and 3) levels of genetic variability are frequently correlated to many characteristics that are important determinants of ecological functioning of populations and of concern to natural resource managers. Although the correlation of genetic variability and phenotypic characteristics do not usually explain a large proportion of the total variation, each correlation may be somewhat independent such that the overall effects on the ecologieal dynamics of the population function are very important.

White-tailed deer show a surprising amount of spatial genetic heterogeneity even in areas like the SRS where the habitats are not severely fragmented. In areas where forested habitats are becoming even more fragmented (Harris 1984), spatial heterogeneity in gene frequency may be further increased. Spatial genetic heterogeneity needs to be taken into account in defining boundaries of management units. In addition, conservation efforts need to recognize that many forms of a species having unique combinations of genes may occur in subpopulations separated by short distances. Spatial heterogeneity in gene frequencies has been recognized in a wide diversity of animals, and its management implications have been recognized as important in fisheries management (Ryman and Utter 1987).

Wide scale fragmentation of forested habitat can lead to reduction of census and effective population sizes, which may fall below the minimum viable size (Soulé 1987). One of the most important long-term effects of falling below the minimum viable population size is stochastic loss of genetic variability, which is important for both the future evolution and the ecological functioning of populations. Small populations may also be more susceptible to the effects of inbreeding, especially if population numbers are reduced quickly and kept low for an extended period of time (Thornhill 1993). Although we do not know whether genetic variability causes changes in population parameters and/or is a result of them, it would seem prudent to manage populations in a way that minimizes the chance of losing genetic variability.

The genetic structure of populations is temporally dynamic over time periods that include the length of typical studies (Smith et al. 1990). This dynamic behavior of populations may result from the interactions from smaller groups that differ from each other genetically. Animals that disperse among these subpopulations to breed may have relatively outbred offspring with higher levels of genetic variability and different phenotypic characteristics than those that breed within the subpopulation in which they were born. Management of forest habitats (e. g., maintaining corridors) to allow this type of dispersal among subpopulations may be essential to the long-term health of many of forest animals (Harris 1984), especially large vertebrates.

One measure of the success of various management programs could be the degree to which we maintain the genetic integrity of

the species. Genetic integrity must not be based on a static concept of the genetic characteristics of the species. Populations are extremely dynamic through space and time, and it seems prudent to manage biological resources so that they continue to exhibit their normal variation in both space and time (NORSE et al. 1986). Thus, we are trying to manage species that are likely to be genetically different in both space and time, and these genetic differences are likely to have direct relationships with biological characteristics important to both the survival of the species and the production of benefits for humans. As human society continues to increase its impact on every habitat on earth, it will be challenging to devise management and conservation strategies for our precious life support systems, especially forests.

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Zusammenfassung

Genetische Heterogenität beim Weißwedelhirsch: Für die Wildbewirtschaftung relevante Erkenntnisse aus einer Langzeitstudie

Daten aus einer Langzeitstudie (16 Jahre) an Weißwedelhirschen (*Odocoileus virginianus*) aus dem Savannah River Site (SRS) des U. S.. Department of Energy wurden im Hinblick auf das Vorkommen von räumlicher und zeitlicher genetischer Heterogenität bei dieser Art analysiert. Die Untersuchung erbrachte drei wesentliche Befunde, die auch für die Bewirtschaftung des Weißwedelhirsches von Bedeutung sind: (1) Wie aus der Analyse von Allozymfrequenzen und mtDNA-Haplotypen hervorging, besteht in Populationen des Weißwedelhirsches eine ausgeprägte räumliche genetische Heterogenität, und zwar auf wesentlich geringerem Raum, als man dies bei einer potentiell so mobilen Art erwarten würde. (2) Die genetische Struktur der Weißwedelhirsche am SRS ist zeitlich unterschiedlich und es gibt eine ausgeprägte Heterogenität zwischen demographischen Entitäten wie Alters- und Geschlechterklassen. (3) Die in elektrophoretischen Untersuchungen ermittelte Heterozygotierate ist häufig mit Merkmalen korreliert, die für die ökologischen Beziehungen in Weißwedelhirschbeständen bedeutsam sind. Diese Befunde wurden im Rahmen eines generellen Bewirtschaftungsmodells für *O. virginianus* evaluiert, das auch für andere Wildtierarten anwendbar ist.

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