

Changes in Artificial Feeding Regulations Impact White-Tailed Deer Fine-Scale Spatial Genetic Structure

JULIE A. BLANCHONG,^{1,2} *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*

KIM T. SCRIBNER, *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*

BRYAN K. EPPERSON, *Department of Forestry, Michigan State University, East Lansing, MI 48824, USA*

SCOTT R. WINTERSTEIN, *Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA*

Abstract

Human activities can change the spatial distribution of individuals within wildlife populations that in turn alters population allele frequencies and spatial genetic structure at fine scales. Artificial feeding is one such activity whose impact on wildlife physical condition, population dynamics, and transmission of disease has been well documented. To evaluate the impact of artificial feeding on the spatial distribution and social organization of white-tailed deer (*Odocoileus virginianus*) we estimated allele frequencies at 3 microsatellite loci for 2,177 hunter-harvested deer and characterized microgeographic genetic structure in 2 regions of the northeast lower peninsula of Michigan, USA, during and following cessation of artificial feeding. While artificial feeding was ongoing we observed no evidence of spatial genetic structure across either region. Spatial homogeneity of allele frequencies over such a large area was surprising given numerous studies that have documented spatial genetic structure in other deer populations, and it was likely a function of the aggregation of multiple kin-structured social groups (i.e., matriline) at artificial feeding sites. Subsequently, when artificial feeding was banned, we found significant genetic differentiation among groups of deer in both regions. Detection of microgeographic genetic structure consistent with a pattern of isolation-by-distance following the ban on artificial feeding was likely the result of increased spatial segregation of social groups of related deer. Our results illustrate how analyses of the degree to which natural populations are spatially genetically structured can be used to infer the effects of human actions on wildlife movement patterns, breeding behaviors, and disease transmission that are difficult to determine using traditional methods. (JOURNAL OF WILDLIFE MANAGEMENT 70(4):1037–1043; 2006)

Key words

artificial feeding, microgeographic genetic structure, microsatellites, Odocoileus virginianus, white-tailed deer.

Humans can have direct and indirect impacts on the demographic and social structure of wildlife populations (Trombulak and Frissell 2000). Harvest, for example, directly impacts population abundance and distribution, sex ratios, and age structure (Kilgo et al. 1998). Human alteration of habitats can affect home-range size, dispersal, and spatial structuring of populations (Hale et al. 2001). Direct and indirect human impacts can also shape the genetic characteristics of a wildlife population (Chesser 1983, McCullough and Chesser 1987, Van Den Bussche et al. 1987). Changes in the size, sex ratio, and age structure of a population can, in turn, change breeding behaviors and mating probabilities that alter population genotype frequencies (Scribner et al. 1991, Scribner 1993). In addition, population genetic diversity and spatial genetic structure are impacted by human actions when dispersal is disrupted, habitat becomes fragmented, and the spatial dispersion of individuals changes (McClenaghan and Truesdale 2002).

White-tailed deer (*Odocoileus virginianus*) often live in close proximity to humans and are directly impacted by human actions such as harvest and artificial feeding (Scribner et al. 1997). Female white-tailed deer live in multigenerational, related female groups (matrilines; Hawkins and Klimstra 1970, McCullough 1979, Marchinton and Hirth 1984) such that genetically related individuals are aggregated in space and segregated from non-related individuals (Mathews and Porter 1993). Characteristics of

deer ecology including site fidelity, female philopatry, and a polygamous mating system result in spatial genetic structure in natural populations (Cronin et al. 1991, Purdue et al. 2000). Specifically, under natural conditions, genetic similarity between individuals or groups in a deer population is expected to decline with increasing geographic distance between them (i.e., isolation by distance).

Numerous studies, however, have documented that human actions that impact characteristics of deer ecology, in turn, affect spatial genetic structure in deer populations (Scribner 1993, Ellsworth et al. 1994, DeYoung et al. 2003). Most of these studies focused on spatial genetic structure among deer populations. Human impacts such as the method and intensity of harvest also affect fine-scale spatial genetic structure within deer populations. For example, Scribner et al. (1997) found significant spatial and temporal variation in microgeographic gene frequencies in a white-tailed deer population that was likely explained by high rates of population turnover, young age structure, and method and intensity of harvest.

White-Tailed Deer in the Northeast Lower Peninsula of Michigan

During the early 20th century, numerous deer hunting clubs were established in the northern lower peninsula of Michigan, USA. Due to high hunting demand and the shortage of natural browse, artificial feeding (i.e., supplemental feeding during the winter and baiting during the hunting season) was widely used to enhance deer population numbers in this region. High deer densities resulting from artificial feeding practices have the potential to have

¹ E-mail: jablanichong@wisc.edu

² Present address: Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA

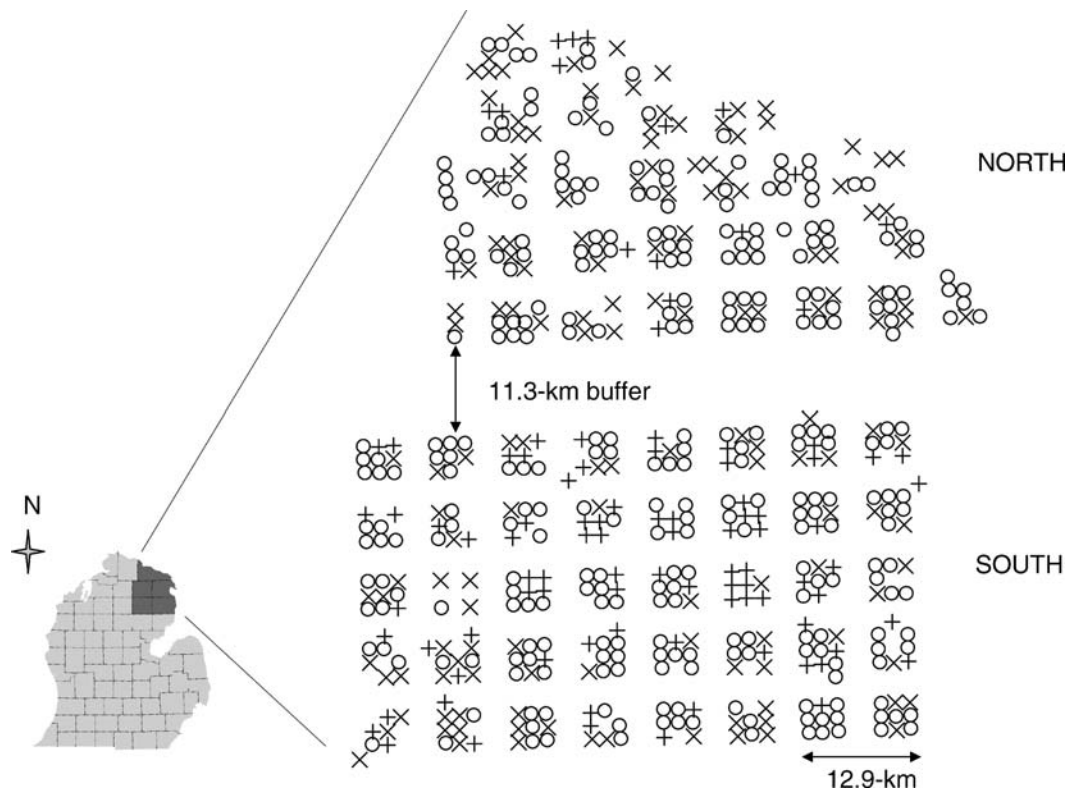


Figure 1. Map depicting the NORTH and SOUTH regions and the 11.3-km buffer zone separating them located in a 5-county area of the northeast lower peninsula of Michigan, USA. Locations of 2.6-km² sampled quadrats are illustrated: x denotes locations sampled only in 1998, + locations sampled only in 2000, and o locations sampled in both years.

negative effects on the natural vegetation (e.g., decreased sapling heights, decreased flowering plants, and increased ferns and grasses; DeCalesta 1994, Chouinard and Filion 2001) and on the deer population in terms of increased transmission and prevalence of disease because artificial feeding concentrates multiple animals (from multiple matriline) at feeding sites (Williams et al. 1993, Smith 2001, Miller et al. 2003).

In the northeast lower peninsula of Michigan, artificial feeding is thought to be responsible for the high prevalence of bovine tuberculosis (*Mycobacterium bovis*; TB) in deer. Artificial food sources resulted in high deer densities (>35/2.6 km²), crowding, and high rates of contact among deer at feeding sites (Schmitt et al. 1997). In an effort to decrease contacts, and thus TB transmission among deer, artificial feeding was banned in northeast Michigan in 1999.

To characterize the effect of artificial feeding on the spatial distribution and social organization of deer, we estimated the degree of spatial variation in allele frequencies among groups of deer harvested within 2 regions of the northeast lower peninsula of Michigan (Fig. 1). Although movements and relationships among harvested deer are unknown, spatial structure can be estimated indirectly by assaying geographic variation of allele frequencies at heritable genetic markers (Scribner et al. 1997). Nonrandom patterns in the spatial distribution of alleles or genotypes can be detected using spatial autocorrelation statistics (Sokal and Oden 1978, Epperson 2003). Because nonrandom patterns of genetic variation are described explicitly as a function of geographic distance, autocorrelation analysis has advantages over standard

techniques such as estimation of variance in allele frequencies (F_{st}), a summary statistic quantifying the overall degree of differentiation among populations (Barbujani 1987, Sork et al. 1999). In addition, while F statistics perform well in the description of historical patterns of gene flow, they are relatively insensitive to small changes in gene frequencies and therefore do not perform as well as descriptors of contemporary microgeographic gene flow. Spatial autocorrelation techniques, on the other hand, can be used to characterize more thoroughly geographic variation in populations and to identify characteristics of populations and the landscapes they inhabit that may be responsible for nonrandom spatial associations (Sokal et al. 1997, Koenig 1999).

Our objective was to evaluate the impact of artificial feeding practices on the spatial distribution and social organization of deer by characterizing and comparing the degree of microgeographic genetic structure of deer in 2 regions of the northeast lower peninsula of Michigan when artificial feeding was ongoing and following the feeding ban. Due to the strong social organization in white-tailed deer, matriline are expected to be spatially segregated (Mathews and Porter 1993). Artificial feeding, however, disrupts the spatial segregation of matriline by bringing individuals from several matriline together in space at feeding sites. Intergroup interactions and spatial overlap among matriline increase when artificial feeding occurs due to the close association of individuals over artificial food (Garner 2001). We expected to find significant differences in the degree of spatial variation in allele frequencies among groups of deer (and inferentially,

Table 1. Number of deer harvested from a 5-county area of the northeast lower peninsula of Michigan, USA, genotyped at 3 microsatellite loci, proportion of females and males, and number of quadrats in the NORTH^a and SOUTH^b regions during 1998 and 2000.

Region	Year	No. of deer genotyped	Proportion F:M	No. of quadrats
NORTH	1998	510	0.56:0.44	202
NORTH	2000	299	0.44:0.56	141
SOUTH	1998	654	0.54:0.46	251
SOUTH	2000	714	0.42:0.58	255

^a NORTH: northern half of the study area where deer experienced lower levels of artificial feeding relative to the SOUTH region.

^b SOUTH: southern half of the study area with a long history of intensive artificial feeding.

significant spatial overlap of matriline) when artificial feeding was ongoing compared with that when artificial feeding was banned. Specifically, we expected to see greater spatial variation in allele frequencies among groups of deer (and inferentially, spatial segregation of matriline) following the ban on artificial feeding relative to when artificial feeding was occurring and animals were aggregated at feeding sites.

Study Area

We divided the northeast lower peninsula of Michigan into 2 regions on the basis of differing histories of artificial feeding (Fig. 1). One region covering 2,323 km² (hereafter, SOUTH region) was located in an area that had a long history of intensive artificial feeding, i.e., hundreds of thousands of kilograms/year for several decades (~0.12 sites/km² based on ~280 sites identified during 1997–1998; Hickling 2002, Miller et al. 2003). The second region (hereafter NORTH region) was located 11.3 km to the north of the SOUTH region and covered 1,994 km² (Fig. 1). The NORTH region experienced lower levels of artificial feeding relative to the SOUTH region (~0.06 sites/km² based on ~115 sites identified during 1997–1998).

Methods

Site Selection

We collected muscle-tissue samples of hunter-harvested deer during the autumn harvest seasons (Oct–Dec) of 1998 when artificial feeding was ongoing and in 2000 when artificial feeding had been banned. Based on data from the Michigan Department of Natural Resources (MDNR) hunter-harvest database, we recorded the 2.6-km² section from which each deer was harvested. We divided the NORTH and SOUTH regions into a grid network of 2.6-km² quadrats separated from one another by at least 2.6 km² (Fig. 1). We sampled all deer samples of either sex (to maximize quadrat sample size) whose harvest locations were within the quadrats contained within the regions described above for analyses ($N = 2,177$). The number of 2.6-km² quadrats from which deer we sampled in each region ranged from 141–255 based on the number and location of deer harvested each year (Table 1). In addition, because sampling intensity was a function of hunter harvest, sample sizes were not uniform across quadrats (Table 1).

The large number and small size of quadrats delineated for our study resulted in relatively small sample sizes within each quadrat (average no. of deer/quadrat = 2.54, SE = 0.06). Hence, allele

frequency estimates in any one quadrat were undoubtedly subject to a large sampling error. Statistical power of autocorrelation coefficients, however, increases with the square of the number of pairs of locations (quadrats). Therefore, if we were to increase the dimensions of our quadrats to increase the number of deer within each quadrat we would actually reduce our statistical power (Epperson and Li 1996), as well as lose spatial resolution (i.e., the minimum spatial scale that can be analyzed increases). The degree of uncertainty in allele frequency estimates resulting from smaller quadrats is more than offset by the increased spatial replication.

We extracted DNA from deer tissue using the QIAGEN DNEasy protocol. We amplified 3 moderately polymorphic, biparentally inherited nuclear microsatellite loci (IGF-1, Kirkpatrick 1992; OBCAM, Fries et al. 1993; RT-9, Wilson et al. 1997) in all animals using the polymerase chain reaction (PCR). We separated PCR products using gel electrophoresis on 6% denaturing polyacrylamide gels, visualized using a Hitachi FMBIO-II laser scanner (Hitachi, Alameda, California). We assigned genotypes with reference to base-pair standards and to individuals of known genotype run concurrently on each gel.

Our goal was to obtain spatial autocorrelation estimates averaged over all alleles and loci. While 3 loci may appear to be a small number of loci to screen, Epperson (2004) and Kalinowski (2002) demonstrated that as long as the number of alleles at a locus is >3 or 4 (depending on the array of allele frequencies), the spatial autocorrelation coefficients for different alleles are nearly independent (i.e., the spatial patterns of frequencies of alleles are nearly independent). Hence, results are not dictated by the number of loci as long as the total number of alleles is large. Statistical power in spatial analysis is, in large part, determined by the product of the number of spatial locations squared and the number of alleles (Epperson 2004). Our dataset was very large, and our product is one of the highest reported (Epperson 2004).

Statistical Analyses

We used exact tests described by Guo and Thompson (1992) and implemented in the program GENEPOP (Raymond and Rousset 1995) to estimate levels of gametic disequilibrium to ensure that loci were independent as well as to determine whether observed allele frequencies accurately reflected expectations under Hardy Weinberg equilibrium. We used GENEPOP to estimate observed and expected heterozygosity and allelic diversity for each locus for each region for each year. We calculated allelic richness, a measure of genetic diversity, using the program CONTRIB (Petit et al. 1998) to adjust allelic diversity for sample size differences between years and between regions.

We used genotypes of deer within each quadrat to calculate allele frequencies. We assayed the degree of genetic differentiation among quadrats within each region for each year by measuring the average variance in allele frequencies among all quadrats (F_{st}) (Weir and Cockerham 1984) using the program SPAGeDi (Hardy and Vekemans 2002). In addition, we calculated mean F_{st} estimates and 95% confidence intervals based on 1,000 permutations of individuals across all quadrats for each region and each year. We compared observed mean F_{st} estimates for each region and year with permutation results to calculate the probability that observed variance in allele frequencies among quadrats was significantly different from permuted values.

Table 2. Estimates of observed heterozygosity and allelic richness (\pm SE) for deer harvested from a 5-county area of the northeast lower peninsula of Michigan, USA, from the NORTH^a and SOUTH^b regions in 1998 and 2000.

Region	Year	Expected heterozygosity		Observed heterozygosity		Allelic richness	
		zygosity	SE	zygosity	SE	richness	SE
NORTH	1998	0.814	0.040	0.803	0.023	9.26	0.06
NORTH	2000	0.809	0.046	0.778	0.032	8.67	0.03
SOUTH	1998	0.801	0.052	0.760	0.046	9.16	0.06
SOUTH	2000	0.801	0.048	0.778	0.047	9.33	0.07

^a NORTH: northern half of the study area where deer experienced lower levels of artificial feeding relative to the SOUTH region.

^b SOUTH: southern half of the study area with a long history of intensive artificial feeding.

We also used allele frequencies of deer within quadrats to estimate Cavalli-Sforza Edwards chord distances (genetic distance; Cavalli-Sforza and Edwards 1967) between quadrats of deer for each region and for each year using the program BIOSYS (Swofford and Selander 1981) or the program PHYLIP 3.5 (Felsenstein 1993). We used Universal Transverse Mercator coordinates to calculate Euclidean distances (geographic distance) between quadrats using the program PASSAGE (Rosenberg 2000). We implemented Mantel tests (Smouse et al. 1986) in PASSAGE to estimate the overall relationship between genetic distance and geographic distance based on matrices constructed from all pairwise comparisons of quadrats within each region for each year. We evaluated significance of correlations between genetic and geographic distance for each region as a whole for each year through randomization (1,000 permutations).

In addition to the overall magnitude of spatial autocorrelation (global) in allele frequencies in each region in each year, we characterized genetic relationships among quadrats of deer separated by a series of successively larger geographic distance classes (local spatial autocorrelation). To calculate the degree of spatial autocorrelation in allele frequencies among quadrats within a single distance class, we estimated normalized Mantel correlations between the full matrix of genetic distances among quadrats and a connectivity matrix in which only pairs of quadrats of deer separated by the geographic distance class of interest were given an indicator value of one, while all other pairs of quadrats were given a value of zero and, thus, excluded from the correlation calculation at that distance class. For each distance class, we evaluated significant difference of correlations among quadrats from zero through randomization (1,000 permutations). We constructed correlogram plots of the Mantel correlation coefficient at each distance class to summarize spatial patterns of genetic

variation for each region (NORTH and SOUTH) for each year (1998 and 2000).

Results

Genotypic frequencies for each locus within each region were consistent with Hardy Weinberg expectations, and loci were in linkage equilibrium (all $P > 0.05$). The number of alleles per locus was 18, 10, and 10 for IGF-1, OBCAM, and RT9, respectively. Because extremely rare alleles are uninformative and potentially biased (Epperson 2004), we removed individuals possessing unique or extremely rare alleles (frequency < 0.001) from subsequent analyses (2 deer from NORTH 1998, 1 deer from SOUTH 2000). Additionally, we binned 4 rare alleles (frequency < 0.002) at the IGF-1 locus with the next-largest-size allele. Heterozygosity and allelic richness were high in NORTH and SOUTH regions (Table 2). Regions (years combined) did not differ from one another in heterozygosity ($t = 0.737$, $df = 2$, $P = 0.538$) or allelic richness ($t = -0.157$, $df = 2$, $P = 0.889$).

Prior to the ban on artificial feeding (1998), we found that the degree of genetic differentiation among quadrats of deer as measured by allelic variance (F_{st}) was not significantly different from zero based on random permutation of individuals across quadrats in either the SOUTH or NORTH regions (Table 3). The near-zero F_{st} values indicate a lack of detectable genetic differentiation among quadrats of deer when artificial feeding was ongoing. Following the ban on artificial feeding (2000), we found population genetic structure (F_{st}) that was significantly different from values based on random permutation (> 0) in the NORTH region, but not in the SOUTH region (Table 3). Based on the average of all pairwise comparisons among quadrats, therefore, we found that the NORTH region in 2000 was the only region to show evidence of significant genetic differentiation (Table 3).

Similar to our findings based on F statistics, but with an explicit consideration of the geographic location of quadrats, using Mantel tests we found no significant genetic differentiation among quadrats of deer as a function of geographic distance in either the NORTH or SOUTH regions in 1998. Specifically, prior to the ban on artificial feeding, there was not a significant relationship between genetic differentiation among quadrats of deer and their geographic distance from each other in either region (Table 4). Using correlation coefficients calculated among quadrats of deer separated by a series of increasing distance classes we did not detect evidence of isolation by distance (Fig. 2a). The lack of detectable spatial genetic structure in either region was likely due to spatial overlap of multiple matrilineal lines at artificial

Table 3. Measures of allelic variance among quadrats of deer (F_{st}) harvested from a 5-county area of the northeast lower peninsula of Michigan, USA, in the NORTH^a and SOUTH^b regions during 1998 and 2000. The F_{st} values reported are for each locus, the observed mean, as well as the permuted mean and its 95% CI based on 1,000 permutations of individuals across all quadrats. The P value indicates the probability that the observed mean F_{st} is not significantly different from the permuted mean.

Region	Year	IGF-1	Locus OBCAM	RT9	Observed \bar{x}	Permuted \bar{x}	Permuted 95% CI	P value
NORTH	1998	0.007	0.001	0.003	0.005	-0.0003	-0.013-0.012	0.41
NORTH	2000	0.027	0.028	0.025	0.027	0.0002	-0.019-0.019	0.01
SOUTH	1998	0.003	-0.003	0.001	0.001	0.0001	-0.011-0.011	0.92
SOUTH	2000	0.006	0.001	0.004	0.004	0.0001	-0.010-0.010	0.42

^a NORTH: northern half of the study area where deer experienced lower levels of artificial feeding relative to the SOUTH region.

^b SOUTH: southern half of the study area with a long history of intensive artificial feeding.

Table 4. Overall (global) correlation between genetic differentiation and geographic distance among quadrats of deer harvested from a 5-county area of the northeast lower peninsula of Michigan, USA, in the NORTH^a and SOUTH^b regions during 1998 and 2000. Statistical significance was evaluated using permutation tests (1,000 replicates).

Region	Year	Correlation	P value
NORTH	1998	0.02	0.20
NORTH	2000	0.09	0.01
SOUTH	1998	-0.01	0.69
SOUTH	2000	0.06	0.01

^a NORTH: northern half of the study area where deer experienced lower levels of artificial feeding relative to the SOUTH region.

^b SOUTH: southern half of the study area with a long history of intensive artificial feeding.

feeding sites. Following the ban on artificial feeding, however, we found a significant correlation between the magnitude of genetic differentiation among quadrats of deer and the geographic distance among quadrats in both regions (Table 4). This differentiation was likely the result of increasing spatial segregation of matriline in the absence of artificial feeding. We found that the degree to which quadrats of deer were genetically differentiated increased with increasing spatial separation in the NORTH and the SOUTH regions in 2000, consistent with a pattern of isolation by distance. Specifically, we found that allele frequencies of deer in quadrats separated by short geographic distances were significantly correlated (>0), while correlations among quadrats of deer separated by greater geographic distances were significantly <0 (Fig. 2b).

Discussion

Despite very large sample sizes and fine spatial resolution, using both F statistics and spatial autocorrelation analyses, we did not detect evidence of microgeographic genetic structure in white-tailed deer populations in 2 studied regions of the northeast lower peninsula of Michigan, USA, during the period when deer were artificially fed. This was a surprising result given that previous studies have documented spatial genetic structure in other free-ranging deer populations (e.g., Mathews and Porter 1993, Scribner et al. 1997). The absence of detectable significant spatial genetic structure in either region's deer population in 1998 is consistent with aggregation of individuals from multiple matriline at artificial feeding sites. Following the ban on artificial feeding, using spatial autocorrelation analysis we found a significant increase in genetic differentiation among quadrats of deer with increasing geographic distance in both regions. The spatial genetic structure we detected in the NORTH and SOUTH regions in 2000 is most likely explained by increased spatial segregation of matriline in the absence of artificial feeding sites. It is important to note that the rapid emergence of detectable spatial genetic structure following the ban on artificial feeding indicates that artificial feeding did not disrupt matrilineal social organization itself, but rather altered the way these matriline used space (i.e., aggregation of multiple matriline at feeding sites). If the social organization of deer had actually been altered by artificial feeding, it would likely have taken several generations for the spatial genetic structure we observed after a single year following the ban on feeding to emerge.

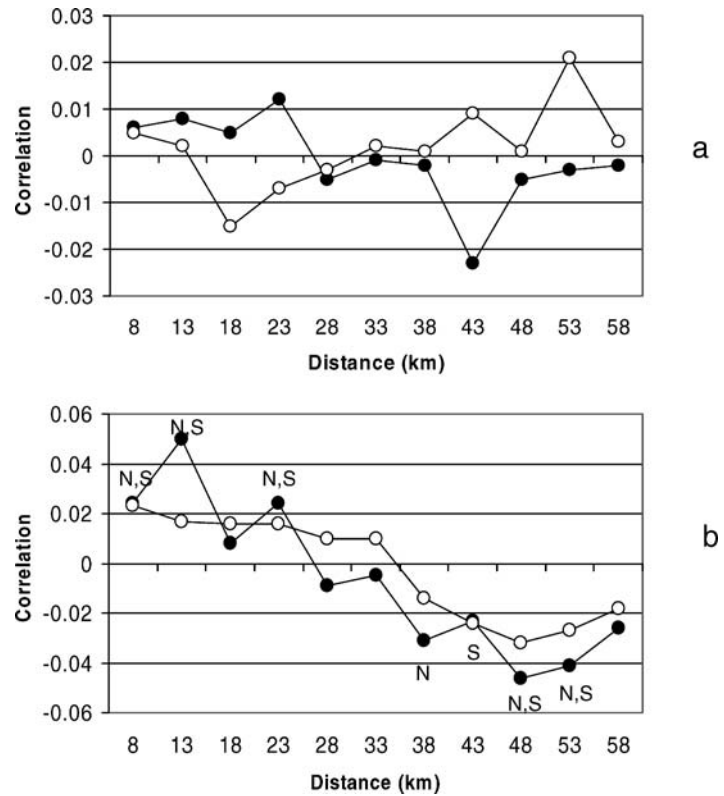


Figure 2. Correlation in allele frequencies between quadrats of deer separated by a series of successively larger distance classes for the NORTH (closed circles) and SOUTH (open circles) regions in a 5-county area of the northeast lower peninsula of Michigan, USA. In 1998, there was no significant relationship between the degree to which quadrats of deer were genetically differentiated and geographic distance in either region (a). In 2000, correlation in allele frequencies between quadrats of deer decreased with increasing geographic distance in both regions (b). Distance classes at which correlations were significantly different from zero are indicated by N for the NORTH region and S for the SOUTH region.

The difference in results we obtained for the SOUTH region in 2000 using F statistics compared with spatial autocorrelation analysis is interesting. There is increasing evidence that F statistics are not ideally suited for measuring ecological (contemporary) gene flow (Sork et al. 1999). Our failure to detect significant spatial genetic structure in the SOUTH region in 2000 based on estimates of F_{st} may be a function of this statistic's relative insensitivity to small changes in gene frequencies that occur over short time scales such as those in our study.

Regardless of the metric used, we found that the magnitude of spatial heterogeneity in gene frequencies (i.e., degree of spatial structure) was higher in deer in the NORTH region than in the SOUTH region in both years. The difference in the degree of spatial genetic structuring between the regions may be a function of differences in historical artificial-feeding intensity. The deer in the 2 regions at the 2 time periods may represent points in a continuum. Specifically, following the ban on artificial feeding, spatial genetic structure, presumably due to the spatial dispersion of matriline, increased in both regions; however, structure in the SOUTH region was still lower than in the NORTH region. Telemetry studies of the deer population in the SOUTH region documented that when artificial feeding was occurring, deer moved extremely short distances relative to those documented in

deer elsewhere in the United States (Garner 2001). The lower degree of spatial genetic structuring in the SOUTH region may be a function of long-standing concentrations of multiple matriline within relatively small areas when artificial food was abundant. Based on our results, it may be predicted that the degree of spatial genetic structure in the SOUTH region will continue to increase as a more traditional matrilineal spatial structure rebuilds in the region in the additional years following the ban on artificial feeding.

Management Implications

The impacts of artificial feeding on wildlife physical condition, movement patterns, social structure, and disease transmission have been well documented (see Dunkley and Cattet 2003 for a comprehensive review). For the deer populations that we considered, the aggregation of multiple matriline at artificial feeding sites obscured evidence of spatial genetic (primarily social) structuring in the population. Importantly for the understanding and control of disease, feeding also likely affected the routes by which bovine TB was transmitted in the population by facilitating transmission of bovine TB among matriline that, under normal conditions, would rarely come into contact (Schmitt et al. 1997,

Palmer et al. 2004). With the ban on artificial feeding, increased spatial segregation of matriline is expected to result in reduced contact and, thus, reduced disease transmission among matriline, such that future disease transmission will likely be concentrated within matriline. We have demonstrated how molecular genetic markers can be useful tools for characterizing fine-scale spatial structure in a wildlife population in order to infer the impact of human actions and management scenarios on wildlife ecology that would be difficult to determine using traditional methods alone.

Acknowledgments

Financial support was provided by the Wildlife Division of the MDNR through the Federal Aid in Wildlife Restoration Act under Pittman-Robertson project W-129-R-17. We thank Wildlife Division personnel for database assistance. We also thank the Michigan Animal Health Diagnostic Laboratory, particularly Dr. S. Fitzgerald, for use of their facilities during sample collection. We also thank numerous Michigan State University undergraduates for help collecting deer tissue. We acknowledge the technical assistance of S. Libants. Comments by 2 anonymous reviewers improved the manuscript.

Literature Cited

- Barbujani, G. 1987. Autocorrelation of gene frequencies under isolation-by-distance. *Genetics* 117:777–782.
- Cavalli-Sforza, L. L., and A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. *Evolution* 21:550–570.
- Chesser, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. *Evolution* 37:320–331.
- Chouinard, A., and L. Filion. 2001. Detrimental effects of white-tailed deer browsing on balsam fir growth and recruitment in a second growth stand on Anticosti Island, Quebec. *Ecoscience* 8:199–210.
- Cronin, M. A., M. E. Nelson, and D. F. Pac. 1991. Spatial heterogeneity of mitochondrial DNA and allozymes among populations of white-tailed deer and mule deer. *Journal of Heredity* 82:118–127.
- DeCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58:711–717.
- DeYoung, R. W., S. Demarais, R. L. Honeycutt, A. P. Rooney, R. A. Gonzales, and K. L. Gee. 2003. Genetic consequences of white-tailed deer (*Odocoileus virginianus*) restoration in Mississippi. *Molecular Ecology* 12:3237–3252.
- Dunkley, L., and M. R. L. Cattet. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Centre, Saskatoon, Canada.
- Ellsworth, D. L., R. L. Honeycutt, N. J. Silvy, M. H. Smith, J. W. Bickham, and W. D. Klimstra. 1994. White-tailed deer restoration to the southeastern United States—evaluating genetic variation. *Journal of Wildlife Management* 58:686–697.
- Epperson, B. K. 2003. Covariances among join-count spatial autocorrelation measures. *Theoretical Population Biology* 64:81–87.
- Epperson, B. K. 2004. Multi-locus estimation of genetic structure within populations. *Theoretical Population Biology* 65:227–237.
- Epperson, B. K., and T. Q. Li. 1996. Measurement of genetic structure within populations using Moran's spatial autocorrelation statistics. *Proceedings of the National Academy of Sciences of the United States of America* 93:10528–10532.
- Felsenstein, J. 1993. PHYLIP (phylogeny interface package) version 3.5. Distributed by the author. Department of Genetics, University of Washington, Seattle, USA.
- Fries, R., A. Eggen, and J. E. Womack. 1993. The bovine gene map. *Mammal Genome* 4:405–428.
- Garner, M. S. 2001. Movement patterns and behavior at winter feeding and fall baiting stations in a population of white-tailed deer infected with bovine tuberculosis in the northeastern lower peninsula of Michigan. Dissertation, Michigan State University, East Lansing, USA.
- Guo, S. W., and E. A. Thompson. 1992. Performing the exact test of Hardy-Weinberg proportions for multiple alleles. *Biometrics* 48:361–372.
- Hale, M. L., P. W. W. Lurz, M. D. F. Shirley, S. Rushton, R. M. Fuller, and K. Wolff. 2001. Impact of landscape management on the genetic structure of red squirrel populations. *Science* 293:2246–2248.
- Hardy, O. J., and X. Vekemans. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2:618–620.
- Hawkins, R. E., and W. D. Klimstra. 1970. A preliminary study of the social organization of white-tailed deer. *Journal of Wildlife Management* 34:407–419.
- Hickling, G. J. 2002. Dynamics of bovine tuberculosis in wild white-tailed deer in Michigan. Michigan Department of Natural Resources, Wildlife Division Report no. 3363, Lansing, USA.
- Kalinowski, S. T. 2002. How many alleles per locus should be used to estimate genetic distances? *Heredity* 88:62–65.
- Kilgo, J. C., R. F. Labisky, and D. E. Fritzen. 1998. Influences of hunting behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology* 12:1359–1364.
- Kirkpatrick, B. W. 1992. Identification of a conserved microsatellite site in the porcine and bovine insulin-like growth factor-1 gene 5' flank. *Animal Genetics* 23:543–548.
- Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution* 14:22–26.
- Marchinton, R. L., and D. H. Hirth. 1984. Behavior. Pages 129–168 in L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole, Harrisburg, Pennsylvania, USA.
- Mathews, N. E., and W. F. Porter. 1993. Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack mountains. *Journal of Mammalogy* 74:33–43.
- McClenaghan, L. R., and H. D. Truesdale. 2002. Genetic structure of endangered Stephens' kangaroo rat populations in southern California. *Southwestern Naturalist* 47:539–549.
- McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a k-selected species. University of Michigan, Ann Arbor, USA.
- McCullough, D. R., and R. K. Chesser. 1987. Genetic variation within and among populations of the Mexican prairie dog. *Journal of Mammalogy* 68:555–560.
- Miller, R. A., J. B. Kaneene, S. D. Fitzgerald, and S. M. Schmitt. 2003.

- Evaluation of the influence of supplemental feeding of white-tailed deer (*Odocoileus virginianus*) on the prevalence of bovine tuberculosis in the Michigan wild deer population. *Journal of Wildlife Diseases* 39:84–95.
- Palmer, M. V., W. R. Waters, and D. L. Whipple. 2004. Shared feed as a means of deer-to-deer transmission of *Mycobacterium bovis*. *Journal of Wildlife Diseases* 40:87–91.
- Petit, R. J., A. El Mousadik, and O. Pons. 1998. Identifying populations for conservation on the basis of genetic markers. *Conservation Biology* 12:844–855.
- Purdue, J. R., M. H. Smith, and J. C. Patton. 2000. Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. *Journal of Mammalogy* 81:179–185.
- Raymond, M., and F. Rousset. 1995. GENEPOP (Version 1.2). Population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248–249.
- Rosenberg, M. S. 2000. PASSAGE. Pattern analysis, spatial statistics, and geographic exegesis. Version 1.0. Department of Biology, Arizona State University, Tempe, USA.
- Schmitt, S. M., S. D. Fitzgerald, T. M. Cooley, C. S. Bruning-Fann, L. Sullivan, D. Berry, T. Carlson, R. B. Minnis, J. B. Payeur, and J. Sikarskie. 1997. Bovine tuberculosis in free-ranging white-tailed deer from Michigan. *Journal of Wildlife Diseases* 33:749–758.
- Scribner, K. T. 1993. Conservation genetics of managed ungulate populations. *Acta Theriologica* S2:89–101.
- Scribner, K. T., M. H. Smith, and R. K. Chesser. 1997. Spatial and temporal variability of microgeographic structure in white-tailed deer. *Journal of Mammalogy* 78:744–755.
- Scribner, K. T., M. H. Smith, R. A. Garrot, and L. H. Carpenter. 1991. Temporal, spatial and age-specific changes in genotypic composition of mule deer. *Journal of Mammalogy* 72:126–137.
- Smith, B. L. 2001. Winter feeding of elk in western North America. *Journal of Wildlife Management* 65:173–190.
- Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35:627–632.
- Sokal, R. R., and N. L. Oden. 1978. Spatial autocorrelation in biology. I. Methodology. *Biological Journal of the Linnean Society* 10:199–228.
- Sokal, R. R., N. L. Oden, and B. A. Thomson. 1997. A simulation study of microevolutionary inferences by spatial autocorrelation analysis. *Biological Journal of the Linnean Society* 60:73–93.
- Sork, V. L., J. Nason, D. R. Campbell, and J. F. Fernandez. 1999. Landscape approaches to historical and contemporary gene flow in plants. *Trends in Ecology and Evolution* 14:219–224.
- Swofford, D. L., and R. K. Selander. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics. *Journal of Heredity* 72:281–283.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- Van Den Bussche, R. A., M. J. Hamilton, R. K. Chesser, and K. T. Scribner. 1987. Genetic differentiation among cottontails from isolated playa basins. *Genetica* 75:153–157.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- Williams, E. S., E. T. Thorne, S. L. Anderson, and J. D. Herriges. 1993. Brucellosis in free-ranging bison (*Bison bison*) from Teton County, Wyoming. *Journal of Wildlife Diseases* 29:118–122.
- Wilson, G. A., C. Strobeck, L. Wu, and J. W. Coffin. 1997. Characterization of microsatellite loci in caribou, *Rangifer tarandus*, and their use in other artiodactyls. *Molecular Ecology* 6:697–699.

Associate Editor: DeWoody.