



Research Article

Influence of Landscape Features on Spatial Genetic Structure of White-Tailed Deer in Human-Altered Landscapes

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ABSTRACT Predictive relationships between estimates of functional population connectivity and physical and biotic landscape features can provide important insights into present and future population responses to human-mediated landscape change. Quantification of associations between landscape features and dispersal or genetic surrogates such as gene flow among areas can be particularly challenging for continuously distributed and highly mobile wildlife species. We assessed the relative influence of natural and human-altered landscape features on white-tailed deer (*Odocoileus virginianus*) spatial genetic structure (SGS) in southern Michigan (USA) using 7 microsatellite markers assayed for 326 adult individuals from 21 contiguous counties (33,284 km²). We used previously collected telemetry data to quantify probabilities of habitat occupancy and seasonal movements that allowed selection and weighting of landscape features to create habitat suitability indices (HSI). We assigned individuals to groups ($n = 13$) for statistical analyses quantifying relationships between measures of SGS (response variable) with Euclidean distance, least cost distances parameterized using HSI, and presence of natural (rivers) and man-made (roads) barriers to dispersal. Over the entire study area, genetic differentiation was significant (mean $F_{st} = 0.019$, $P < 0.001$) and increased with increasing inter-group geographic distance ($r^2 = 0.381$; $P < 0.05$). We identified features in the landscape matrix between groups including rivers, high traffic roads, and habitats of intermediate HSI as inhibiting gene flow. Low HSI was associated with low between-group F_{st} and appeared to facilitate gene flow. Quantification of the relative importance of man-made barriers (roads) and habitat suitability to SGS for white-tailed deer emphasizes the importance of joint use of ecological and genetic analyses in conservation and control efforts for abundant and mobile wildlife species. © 2014 The Wildlife Society.

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Landscape composition and configuration typically vary over space and time (Wagner and Fortin 2005) because of natural processes that have occurred over historical and contemporary time scales (Anderson et al. 2010) and because of recent human activities (D-Eon et al. 2002). Increasingly, landscape changes are occurring on ecological time scales because human activities have left a more recent and expansive footprint on landscape features than have natural processes (Kareiva et al. 2007). These recent events including creation of roads (Forman and Alexander 1998, Balkenhol and Waits 2009) or changes in environmental conditions and land-use (Geffen et al. 2004, Coulon et al. 2006) affect probabilities of habitat occupancy and rates of gene

flow among wildlife populations. Understanding how landscape features and aspects of a species' ecology affect movement patterns and population connectivity is a major challenge facing wildlife conservation and management programs attempting to maintain ecological integrity (Andreasen et al. 2001), functional connectivity (Beier et al. 2008), population viability (Hanski 2002), or to minimize human conflicts (Henderson et al. 2000). Further, landscape features can act as agents of selection (Manel et al. 2010). Therefore, characterizing rates of dispersal through heterogeneous landscapes is important to detect selection along environmental gradients (De Mita et al. 2013), and is increasingly possible because genomics data is becoming available for many organisms, including ungulates (Haynes and Latch 2012).

Natural and anthropogenic processes have affected physical and biotic landscape features that concurrently have influenced wildlife population demography and individual movements (Clobert et al. 2009). These processes can, in

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turn, influence levels of genetic variability within populations and the degree of spatial variation in population gene frequency (i.e., operational definition of spatial genetic structure [SGS]; Waples and Gaggiotti 2006, Boulet et al. 2007). For instance, features of the physical and biotic environment such as habitat quality may affect the probability of movements such as dispersal (Bowler and Benton 2005). Habitat quality considers multiple components collectively (i.e., food, cover) to evaluate the capacity of an area to support individuals. As habitat quality varies spatially, individuals are likely to remain in areas (patches) of high habitat quality (Knowlton and Graham 2010) and disperse into or through areas of lower habitat quality. Thus, if individuals are philopatric to natal areas, expectations are that areas of comparatively higher and lower habitat quality will be characterized by higher and lower measures of genetic diversity, respectively (Epperson 1993), including mean relatedness. For example, areas of higher habitat quality may support higher population densities and individual fitness. Likewise, areas of lower habitat quality may demonstrate lower levels of genetic diversity due to smaller population sizes and decreased fitness (Morris et al. 2004). These lower quality areas may also exhibit higher levels of gene flow as individuals disperse through and potentially seek areas of higher quality habitat (Morris et al. 2004). Other landscape features such as roads (Balkenhol and Waits 2009) and rivers (Blanchong et al. 2008) may present barriers to dispersal, and thus affect SGS.

For species that disperse long distances or are widely distributed throughout the landscape, measures of genetic distance or spatial variance in allele frequency (e.g., F -statistics; Weir and Cockerham 1984) are often used to characterize gene flow among groups of animals captured from different locales (Cushman et al. 2006, McRae and Beier 2007, Purrenhage et al. 2009). Accordingly, landscape genetic studies (Manel et al. 2003; Storfer et al. 2007, Holderegger and Wagner 2008) using estimates of SGS and remotely sensed spatial data describing landscape features are increasingly emphasized as an effective means to quantify the relative importance of factors affecting connectivity among populations (Cushman et al. 2006, Hall and Bessinger 2014). As wildlife populations are increasingly affected by human activities and landscape changes (Fahrig 2007), understanding the complex interactions between measures of SGS, geographic distance, and landscape permeability is critical for management or conservation planning (Minor and Urban 2007, Kool et al. 2010), and population control (Côté et al. 2004).

The genetic signatures of population responses to human activities are often dependent on a species' vagility (Landguth et al. 2010a,b). White-tailed deer (*Odocoileus virginianus*) are highly mobile habitat generalists (Hirth 1977) that have successfully adapted to human-altered landscapes including areas interspersed with forest cover, edge (Marchinton and Hirth 1984, Shi et al. 2006), agricultural crops that supplement natural forage (Gladfelter 1984), and urban areas (Blanchong et al. 2013). White-tailed deer population abundance has increased from

historical (pre-settlement) levels in southern Michigan, USA (Michigan Department of Natural Resources [MDNR] 2009). In southern Michigan and many areas in the north-central United States and southern Canada, historically forested landscapes have been fragmented by agricultural practices and human developments such as transportation networks that have created an increasing footprint of urbanization over the past 150 years (Hawbacker et al. 2006). High levels of abundance do not alone imply that dispersal across anthropogenically altered landscapes is extensive. Therefore, management and control activities for natural populations of ecologically and economically important species such as white-tailed deer necessitate a greater understanding of how landscape features affect movements (With et al. 1997, Crooks and Sanjayan 2006).

Our general objective was to quantify relationships between natural landscape features and features associated with past and present human activities and SGS of white-tailed deer in southern Michigan. We hypothesized that landscape features reflecting the quality and spatial heterogeneity (Diefenbach et al. 2008) and degree of habitat fragmentation (Long et al. 2005), that are common in the north-central United States and Michigan are associated with SGS.

Specifically, our working hypotheses were 1) habitat suitability within patches occupied by white-tailed deer was positively related to genetic diversity and SGS, 2) measures of habitat suitability and landscape resistance between populations were better predictors of genetic diversity and SGS than geographic distance alone, and 3) natural landscape features including rivers as well as prominent and recent human construction (highways) were barriers to movements such as dispersal, as reflected by estimates of SGS.

STUDY AREA

We conducted the study across 21 counties (33,284 km²) in southern Michigan. The area is a fragmented mosaic of land-cover and land-use practices, dominated by agricultural cropland planted predominately in corn and soybeans, particularly in the central region of the study area. Natural vegetation including deciduous upland and lowland hardwood habitat types were more abundant in the western, eastern, and northern portions of the study area. The growing season (i.e., the average annual accumulation of daily mean temperatures >5.6°C) was 150 days, generally occurring between mid-May to mid-October (Sommers 1977). Average annual snowfall was 120.2 cm between 1999 and 2000 (Midwestern Regional Climate Center, Champaign, Illinois, USA). Deer densities within the study area range from 15 to 40 deer/km²; densities were higher in areas with limited hunting access (MDNR 2010). Because winter thermal cover may not be necessary for deer in this area (Torgersen and Porath 1984), individuals tend to be non-migratory between summer and winter ranges (Pusateri 2003, Hiller 2007).

METHODS

Development of Indices of Habitat Suitability

Habitat suitability indices are frequently used to identify characteristics of areas that are selected by wildlife (Morrison et al. 2006). Radio-telemetry data are often used to develop habitat suitability indices (Aebischer et al. 1993, Epps et al. 2007, Chietkiewicz and Boyce 2009, review of applications with genetic data in Spear et al. 2010). We used previous radio-telemetry data on white-tailed deer within 2 portions of our study area (Pusateri 2003, Hiller 2007) to identify and weight landscape features that have been identified as features important for determining deer habitat selection during all seasons in southern Michigan (Miranda and Porter 2003, Hiller 2007). The studies used 59 adult deer captured during winter 2001–2002 (Pusateri 2003, Michigan State University All-University Committee on Animal Use and Care approval 01/01–001-00) and 66 adult deer captured during winter 2004–2006 (Hiller 2007, Michigan State University All-University Committee on Animal Use and Care approval 01/04–006-00) located 2–5 times/week during the entire year using triangulation methods (White and Garrott 1990). The number of location estimates averaged 132/deer (Hiller 2007).

We obtained characterization of white-tailed deer habitat suitability in southern Michigan landscapes using land cover classifications from the Integrated Forest Monitoring, Assessment, and Prescription (IFMAP) data (MDNR 2003) at a resolution of 30-m × 30-m in ArcGIS 9.3.1 (Environmental Systems Research Institute, Redlands, California, USA). We used the specified resolution because the IFMAP data was classified from Landsat Thematic Mapper satellite imagery produced in 30-m × 30-m cells. We estimated a composite habitat suitability value based on the proportion of area classified as urban, coniferous, upland deciduous, woody wetland, and agricultural edge within a circular moving window with a radius of 900 m. A 900-m radius window was comparable to the home range size of a typical adult female deer in Michigan (Pusateri 2003, Hiller 2007). The value assigned to each pixel was the habitat suitability within a hypothetical deer's home range if it were centered on any 30-m × 30-m pixel within the study area. Habitat suitability was quantified as:

$$HSI = \frac{(4CONIF) + (2DECID) + (2AGEDGE) + URBAN + WETL}{10}$$

where the habitat suitability index (HSI) was the weighted average of CONIF, DECID, AGEDGE, URBAN, and WETL. Weighting coefficients (Spear et al. 2010) were assigned based on a ranking of importance (relative occupancy time within each habitat type) to deer habitat selection in southern Michigan. The variable CONIF was the suitability index on a scale of 0–100 of the proportion of coniferous forest type within the evaluation area. The minimum threshold for high suitability was 10% of the home range comprised of coniferous forest types (Pusateri 2003, Hiller 2007). The variable DECID was the suitability index for the proportion of deciduous forest cover; optimal

conditions occurred between 20% and 70% (Hiller 2007). AGEDGE was the suitability index quantifying the proportion of agricultural row crops within 180 m from a forest edge. Agricultural crops provide an abundant food source for deer (Gladfelter 1984), and comprise the major portion of their diet (Nixon et al. 1970) and home range (Pusateri 2003, Hiller 2007) in the mid-west agricultural region of the United States. Thus, suitability of AGEDGE increased linearly with percent of agricultural edge. Deer generally do not select residential or urban areas (i.e., areas with man-made structures, roads, golf courses, residential parks; Pusateri 2003, Hiller 2007). However, some low-density residential areas may provide food sources for deer (Miranda and Porter 2003). Therefore, the suitability of URBAN was based on a negative relationship to the percent of residential/urban area within the moving window. The variable WETL was an index quantifying the ideal woody wetland composition within the window, suitability was optimal between 10% and 25% (Pusateri 2003).

We also included in analyses presence–absence of natural landscape features including rivers (Blanchong et al. 2008) and roads (Balkenhol and Waits 2009, Corlatti et al. 2009) that have been found to affect SGS. We classified highways according to levels of use (traffic volume) based on information acquired from the Michigan Department of Transportation Traffic Monitoring Information System (<http://www.michigan.gov/mdot-tmis>). Specifically, we classified major (4 lane) highways as high-traffic (>50,000 vehicles/24 hr), medium traffic (20,000–50,000 vehicles/24 hr), or low traffic (<20,000 vehicles/24 hr). We also used presence of all water bodies classified as rivers according to Michigan hydrology maps (Michigan Center for Geographic Information 2009).

Sampling for Genetic Analysis

Several aspects of study design and genetic analysis can improve inferences regarding the influences of landscape features on spatial genetic structure (Anderson et al. 2010), including the spatial extent, lag, and grain over which observations are collected and analyses conducted (Dungan et al. 2002, Cushman and Landguth 2010). Locations of individual adult (≥ 1.5 yr) deer samples ($n = 326$; 44% female and 56% male) collected over the period 1998–2000 were spatially referenced based on the location of harvest (township, range, section) provided by hunters.

We assigned individuals to groups that were spatially arrayed over contiguous geographic areas to achieve replication for statistical comparisons between measures of spatial genetic structure, inter-group Euclidean distance, inter-group measures of habitat quality (HSI), and presence–absence of dispersal barriers (roads and rivers). Specifically, we assigned individuals to 13 contiguous groups that we defined a priori rather than a posteriori (e.g., using clustering algorithms such as BAPS; Corander Marttinen 2006) because deer in Michigan (e.g., Blanchong et al. 2007) and elsewhere in the Midwestern United States (e.g., Robinson et al. 2012) are continuously distributed and

exhibit a pattern of isolation-by-distance (Wright 1943). We used groups rather than individuals for several reasons. The first is precedence in the landscape genetics literature (Koyghobadi et al. 2005, Goldberg and Waits 2010, Murphy et al. 2010, review in Storfer et al. 2007). Secondly, our deer samples were spatially referenced only to a single (harvest) location, which makes assigning accurate weights, such as habitat suitability difficult. Also, uncertainty may exist regarding the reported harvest locations of individuals, and our harvest locations were reported only to the level of a section (a 2.6-km² area). These problems are less of a concern when characterizing habitat patches and habitat suitability for a group of individuals inhabiting those patches. Mean area sampled per group was 734 km², range 259–1,277 km²; Fig. 1). We assumed the groups were a representative sample to understand the spatial genetic structure of deer within the study area.

We identified boundaries of deer groups in ArcMap using the minimum convex polygon (MCP) method with Hawth's Analysis Tools (Beyer 2004) and connecting points of the outer coordinates of clustered (i.e., based on proximity) deer samples. Group size averaged 25 individuals (range 14–42). Mean inter-group distance was 101 km (range 30–189 km). We calculated the average HSI within the polygon defining the boundary of each group to quantify mean habitat suitability associated with landscapes within each group polygon.

Genetic Analysis

We extracted DNA from archived tissue samples collected from white-tailed deer using QIAGEN DNeasy extraction kits (Qiagen, Valencia, CA). We genotyped all individuals at 7 nuclear, bi-parentally inherited microsatellite loci (BM1225, BM4107, BM4208, BM6506, CSN3, Bishop et al. 1994; RT23, RT27, Wilson et al. 1997). We conducted polymerase chain reactions (PCR) and genotyping following protocols described in Blanchong et al. (2006, 2008). We screened PCR products using either a Li-COR Instruments Li-COR IR² DNA Sequencer (NENTM, Lincoln, NE) or Hitachi Instruments FMBIOII sequencer (Hitachi Software Engineering Co., Ltd., Yokohama, Japan). We ran individuals of known genotype and size standards concurrently on each gel. Two experienced laboratory personnel scored all genotypes. We genotyped 10% of all samples a second time for all loci as a means of quality control. Scoring errors rates were <0.5% (1 of 231 genotypes were erroneous during error check).

For each group of deer, we tested genotype frequencies at all loci for Hardy–Weinberg (HW) expectations using the exact HW test of Guo and Thompson (1992) implemented in GENEPOP version 4.0 (Rousset 2008). We conducted tests for evidence of genotypic linkage disequilibrium (i.e., whether genotypes at 1 locus are independent of genotypes at a second locus) using the log-likelihood ratio test, with probabilities computed based on the Markov chain method of Raymond and Rousset (1995) implemented in GENEPOP. We used a Bonferroni correction (Rice 1989) to adjust alpha levels for multiple tests. We calculated estimates of

allele frequencies and expected and observed heterozygosity (H_E , H_O) for each group using MICROSATELLITE ANALYSER v 3.12 (Dieringer and Schlötterer 2003). We calculated group estimates of allelic richness (A_r) and the inbreeding coefficients (F_{IS}) using FSTAT version 2.9.3 (Goudet 2001). We derived estimates of pairwise relatedness among individuals within each group using maximum likelihood methods (Wagner et al. 2006) implemented in program ML-Relate (Kalinowski et al. 2006). We selected this method because maximum likelihood methods are typically more accurate than other methods (Milligan 2003). Using GENECAP (Wilberg and Dreher 2004; based on the methods of Evett and Wier 1998), we estimated a multi-locus probability of identity at the level of full siblings was 0.000498 over 7 loci.

The quality of habitat within an area occupied by an individual can contribute to decisions to disperse (either immigration or emigration) owing to condition or phenotype-dependent factors (Clobert et al. 2009). Hence, we quantified the relative quality of landscape features (HSI) associated with areas occupied by each group. We used multiple linear regression implemented in SAS (v 9.2 SAS Institute, Inc., Cary, NC) to associate within-group measures of genetic diversity (H_E , mean relatedness and percentage of inter-individual pairs related at half-sibling [HS], full-sibling [FS], or parent-offspring [PO] levels) to HSI. We also used group size (N) and size of the MCP area (km²) encompassing each group as predictor variables to test for their effects. We used Bayesian methods (Foll and Gaggiotti 2006) implemented in program GESTE to determine the influence of mean habitat quality (HSI) within the MCP of each group to genetic differentiation (using point-estimates of F_{st} from GESTE) between the focal group and all other groups. We used a burn-in of 50,000 replicates, a thinning interval of 20, and a sample size of 10,000. We conducted analyses over 250,000 iterations.

Analyses of Spatial Genetic Structure Among Groups

We derived estimates of SGS (F_{st} , Weir and Cockerham 1984) from FSTAT and used them as a measure of SGS for all pair-wise comparisons between the 13 groups. We used Bonferroni corrections (Rice 1989) to adjust alpha levels to account for multiple tests.

To test the hypothesis that the degree of SGS among white-tailed deer in southern Michigan was a function of geographic proximity (isolation-by-distance; Wright 1943, Rousset 1997), we performed a Mantel test of Euclidean distance between group centroids on $F_{st}/(1 - F_{st})$ in PASSaGE version 2 (Rosenberg and Anderson 2011). We assessed statistical significance based on 1000 permutations.

Bayesian clustering methods can have difficulty identifying contiguous genetic clusters of individuals in species and landscape contexts characterized by isolation-by-distance (Waples and Gaggiotti 2006, Guillot et al. 2009). However, to further examine any strong effects of putative barriers (e.g., major highways) that may have overwhelmed an underlying signal of isolation-by-distance, we employed

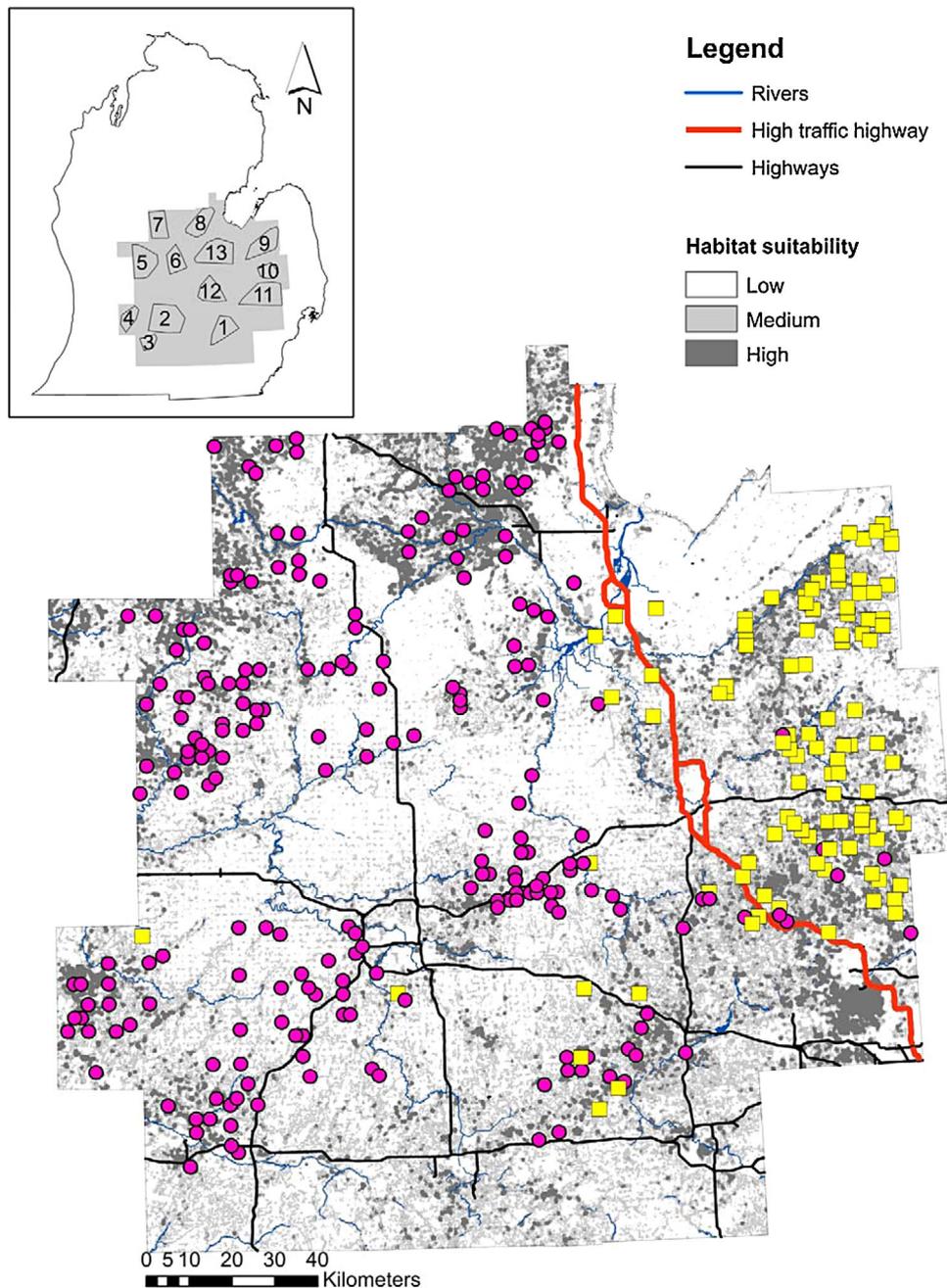


Figure 1. Estimates of habitat suitability (light shade = low; dark shade = high), boundaries of defined deer groups (inset), and collection locations (points) of individuals genotyped in southern Michigan, USA 1998–2000. Membership to 1 of 2 distinct genetic clusters is shown by pink circles or yellow squares. The high-traffic highway refers to the location of Interstate-75 (bold red line).

Bayesian clustering methods that incorporated information on individual harvest location to estimate cluster membership (e.g., Corander and Marttinen 2006, Guillot et al. 2009). We performed analyses using BAPS version 4.0 (Corander et al. 2004), implemented using the spatial genetic mixture analysis to assign individuals to genetic clusters. We completed 10 independent runs of $K = 1-13$, and compared results for consistency.

We tested for spatial genetic autocorrelation using all individuals in GenAlEx 6.5 (Peakall and Smouse 2012) to better understand the distances below which dispersal may be

restricted, and individuals are more genetically related than expected by chance. We tested for significance using 9999 random permutations of the data, and 95% confidence intervals; estimates of r were determined by 9999 bootstraps. We used 10 distance classes at 20-km intervals.

Quantifying Landscape Effects on Measures of Spatial Genetic Structure

To quantify the influence of landscape features on deer SGS, we used cost-distance analysis implemented in ArcMap and the multivariate optimization approach of Pérez-Espona

et al. (2008) to calculate the least cumulative cost of moving through landscapes between the geometric centroids of deer groups. We used several landscape features to calculate the cost distance to assess their influence on deer population structure: major interstate highways (highways classified as high, medium, or low based on traffic volume; see above), rivers (Michigan Center for Geographic Information 2002), and habitat suitability (HSI). We classified habitat suitability into low (0–35.9), intermediate (36–57.9), and high (58–100) by optimizing the goodness of variance fit, and separated classes using Jenk's optimization in ArcMap, which minimized the sum of the variance within each suitability category (Jenks 1967). We classified suitability into the 3 categories to evaluate the specific contribution of different measures of suitability to SGS. Because linear features can become discontinuous when converted to 30-m raster cells in the resistance surface, we buffered rivers, streams, and roads by 50 m prior to converting the linear features to 30-m × 30-m raster format.

We calculated least cost-distance matrices for each landscape feature by developing several cost surfaces and assigning each grid cell a cost = 1, except for those containing the landscape feature of interest (Pérez-Espona et al. 2008). Considerable uncertainty exists associated with weights assigned to landscape variables (Spear et al. 2010, Manel and Holderegger 2013). To address this uncertainty in a systematic and quantitative manner, for the landscape features of interest, we assigned a range of 8 cost values (0.0001, 0.001, 0.01, 0.1, 10, 100, 1,000, 10,000). The range in cost values were as described in other ungulate studies (Pérez-Espona et al. 2008). Values increased incrementally by a power of 10 to ensure we evaluated an adequate range of values to determine whether the features were acting as barriers (cost > 1) or facilitating (cost < 1) gene flow. We used Mantel tests and permutation testing ($n = 1,000$ permutations) in Program R v 3.2.1 to determine which cost value best quantified the effect of each landscape feature on deer SGS, and to quantify the probability the observed results would occur by chance. Additionally, we constructed inter-group matrices of Euclidean distance and genetic distance and used Mantel tests to quantify this relationship. We determined which cost value for each landscape feature maximized the r^2 value and thus explained more of the variability (relative to Euclidean distance alone) in the relationship between genetic differentiation and landscape features (Pérez-Espona et al. 2008).

We then created resistance surfaces for all possible combinations of landscape features using the cost values for each feature that maximized r^2 . We ran 10 Mantel and partial Mantel tests (i.e., partialling out Euclidean distance) to compare which surface best explained SGS. Because of the problem of non-independence of data points, Mantel tests are one of the most appropriate analyses for distance-based data (Legendre and Fortin 2010).

Because the Mantel and partial Mantel tests tend to have high type 1 error rates (Balkenhol et al. 2009) and tend not to correctly estimate r , we also tested the relationship between SGS and all possible combinations ($n = 31$) of landscape

features (with the optimal cost weighting) using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) for multiple regression models. Using multiple methods reduced the chances of leading to erroneous method-dependent conclusions (Balkenhol et al. 2009). We calculated AIC, relative AIC (ΔAIC), model likelihoods, and Akaike weights for each model. We then used the Akaike weights to determine parameter estimates and unconditional standard errors (Burnham and Anderson 2002) and the best-cost model for explaining the relationship between genetic differentiation and landscape features. Because we compared each group with all other groups, spatial autocorrelation in measures of inter-group differentiation may exist and affect evaluations of model fit via AIC (Goldberg and Waits 2010). Thus, we used multiple tests (i.e., Mantel, partial Mantel, AIC) used for analyses to combat shortcomings of any single method.

RESULTS

Spatial Heterogeneity in White-Tailed Deer Habitat Suitability

The quality of deer habitat as reflected in measures of habitat suitability (HSI) varied widely at multiple spatial scales across the study area (Fig. 1) and within areas occupied by each group of deer (Table 1). The central portion of the study area, generally extending from southwest to northeast, was predominantly agricultural lands. Mean HSI estimates for white-tailed deer groups collected from these areas (e.g., groups 2, 6, 12, and 13) were considerably lower than for groups collected in peripheral areas (Table 1). Large contiguous areas of crops were interspersed with comparatively smaller patches composed of small woodlots and woody vegetation associated with wind-rows and riparian corridors as well as highways. Areas to the northwest, south, and east of this central region were composed of higher proportions of woody vegetation and were of comparatively higher habitat quality. The entire study area was bisected by several major highways and rivers (Fig. 1).

Measures of Genetic Diversity Within Groups

Genotypic frequencies at all loci within each white-tailed deer group conformed to HW expectations, and we did not detect any evidence of genotypic disequilibrium. Mean estimates of group genetic diversity varied among groups (allelic richness, A_r : 6.58–9.46, observed heterozygosity H_O : 0.761–0.887, expected heterozygosity H_E : 0.797–0.845, Wright's inbreeding coefficient F_{is} : –0.089 to 0.103; Table 1). We did not observe latitudinal or longitudinal trends in measures of diversity among groups ($P > 0.05$). Mean habitat quality (HSI) within group sampling areas did not predict group measures of genetic diversity (H_E , mean relatedness); however, we found a significant positive relationship between mean group relatedness and group sample size ($r^2 = 0.67$, $P < 0.01$). Collectively, measures of within group genetic diversity were associated with the sample size and/or area but not the quality of habitat within the area encompassing groups.

Table 1. Summary measures of genetic diversity including estimates of inter-individual relatedness within 13 groups of white-tailed deer sampled in southern Michigan, 1998–2000, minimum convex polygon estimates of areas (km²) encompassing all individuals within a group, and mean habitat suitability indices (HSI) in areas encompassing each group. We measured HSI on a scale of 0–100; 100 represents optimal conditions.

Group	Sample size	Measures of genetic diversity ^a					Mean relatedness	Group area	Mean HSI/group area
		<i>k</i>	<i>A</i>	<i>H_O</i>	<i>H_E</i>	<i>F_{is}</i>			
1	19	8.86	9.085	0.887	0.817	-0.089	0.0456	663.02	48.30
2	30	10.14	7.072	0.830	0.844	0.017	0.0556	1,277.16	34.06
3	13	8.14	9.463	0.810	0.831	0.026	0.0341	259.66	46.19
4	17	8.71	6.765	0.787	0.849	0.103	0.0376	390.61	49.75
5	38	10.71	7.648	0.817	0.817	-0.001	0.0525	978.13	45.13
6	14	8.43	7.916	0.837	0.844	0.009	0.0384	541.23	29.28
7	16	8.86	8.402	0.809	0.813	0.005	0.0369	659.72	46.45
8	26	10.43	7.554	0.818	0.815	-0.003	0.0504	702.65	59.59
9	38	10.43	6.577	0.761	0.797	0.045	0.0524	808.06	49.83
10	19	9.57	8.754	0.864	0.838	-0.021	0.0470	342.59	46.34
11	42	11.14	8.611	0.830	0.845	0.018	0.0526	1,129.76	53.34
12	31	10.71	7.669	0.844	0.833	-0.026	0.0535	672.77	35.97
13	19	9.57	8.277	0.807	0.815	0.023	0.0305	1,116.53	37.25

^a*k*, mean number of alleles; *A*, allelic richness; *H_O*, observed heterozygosity; *H_E*, expected heterozygosity; *F_{is}*, Wright's inbreeding coefficient. Statistical significance of *F_{is}* (*P* < 0.05).

Analyses of Spatial Genetic Structure

Genetic differentiation over the entire study was significant (mean inter-group *F_{st}* = 0.019, *P* < 0.01, range 0.000–0.053; Table 2). Deer sampled in the eastern portion of the study area (groups 9 through 11; Fig. 1) were particularly divergent from deer across the central, northern, western, and southern portion of the study area (Table 2). Inter-group genetic differentiation increased when inter-group geographical distance increased (*r*² = 0.186, *P* < 0.05; Fig. 2).

At the level of individuals, Bayesian clustering revealed evidence for 2 genetic clusters. One cluster consisted of individuals primarily centered in the eastern region of the study area predominantly associated with groups 9 through 11 (Fig. 1). The other genetic cluster consisted of individuals that were more widely distributed throughout the south, east, and northern regions of the study area.

Individual relatedness among individuals was significantly spatially autocorrelated over distances within the boundaries of the sampling groups (Fig. 3). However, evidence for gene flow over geographically more expansive areas (Fig. 2) suggests that multi-generational gene flow or

long-distance gene flow is also important to SGS at larger spatial extents.

Effects of Within Patch Habitat Quality on SGS

Deer collected from groups inhabiting areas of lowest and highest habitat quality as reflected by mean group HSI were less genetically differentiated from other groups than groups of deer inhabiting areas of intermediate quality (Fig. 4). However, estimated group HSI was not a significant predictor of SGS (*P* > 0.05), likely owing to the non-linear nature of the relationship between HSI and inter-group *F_{st}* values. The addition of a quadratic term in the regression of inter-population genetic variation and mean population HSI (*r*² = 0.436; *P* < 0.05) had a better fit than the linear model (*r*² = 0.013; *P* > 0.05) suggesting that the relationship between patch habitat quality and propensity for gene flow were neither linear nor positive across the range of the mean HSI values of the 13 sampled groups. This result was consistent with analyses of high, intermediate, and low HSI and SGS (see below). Mean inter-group *F_{st}* differed among groups (Table 2). For

Table 2. Pair-wise genetic differentiation (*F_{st}*; above diagonal) and Euclidean distance (km; below diagonal) between white-tailed deer sampled from 13 groups in southern Michigan, 1998–2000. Values with an asterisk (*) indicate pairwise *F_{st}* values that are significantly different from (*P* < 0.05).

White-tailed deer groups													
	1	2	3	4	5	6	7	8	9	10	11	12	13
1		0.0115	0.0204	0.0127	0.0165*	0.0224*	0.0204	0.0105	0.0286*	0.0299	0.0093	0.0014	0.0039
2	70.53		0.013	0.0185	0.0103	0.0071	0.0151	0.0121*	0.0493*	0.0347*	0.0134	0.0033	0.0086
3	92.44	35.42		0.0152	0.0291*	0.0117	0.0325	0.0309*	0.042	0.0279*	0.0092	0.0099	0.0181
4	115.53	45.3	37.68		0.0291*	0.0192*	0.0368*	0.0269*	0.009	0.0056	0.0074*	0.0131*	0.016
5	128.7	76.43	99.76	72.13		0.0099	0	0.0122	0.0444*	0.0435*	0.0304*	0.0073	0.0082
6	102.73	73.39	105.84	91.03	39.15		0.0164	0.0142	0.0469*	0.0362*	0.0248*	0.0038	0.0105
7	151.82	117.49	145.58	121.02	49.11	49.47		0.013	0.0528*	0.0498*	0.0265*	0.0125	0.0012
8	134.57	126.62	160.64	146.9	84.74	56.03	52.09		0.0436*	0.041*	0.0153*	0.0132*	0
9	116.78	151.55	186.07	188.67	148.8	110.01	131.68	81.78		0.006	0.0213*	0.0350*	0.0322*
10	89.91	137.48	169.83	179	152.31	113.49	146.15	101.92	34.47		0.0100*	0.0296*	0.0231
11	65.14	122.96	152.31	167.04	152.82	116.13	156.17	118.56	63.66	29.89		0.0137*	0.0043
12	49.05	64.33	98.35	105	89.95	64.33	104.8	85.96	87.77	74.01	65.16		0.0031
13	95.04	102.69	138.11	133.92	89.67	50.82	79.28	41.76	59.19	67.03	78.49	48.52	

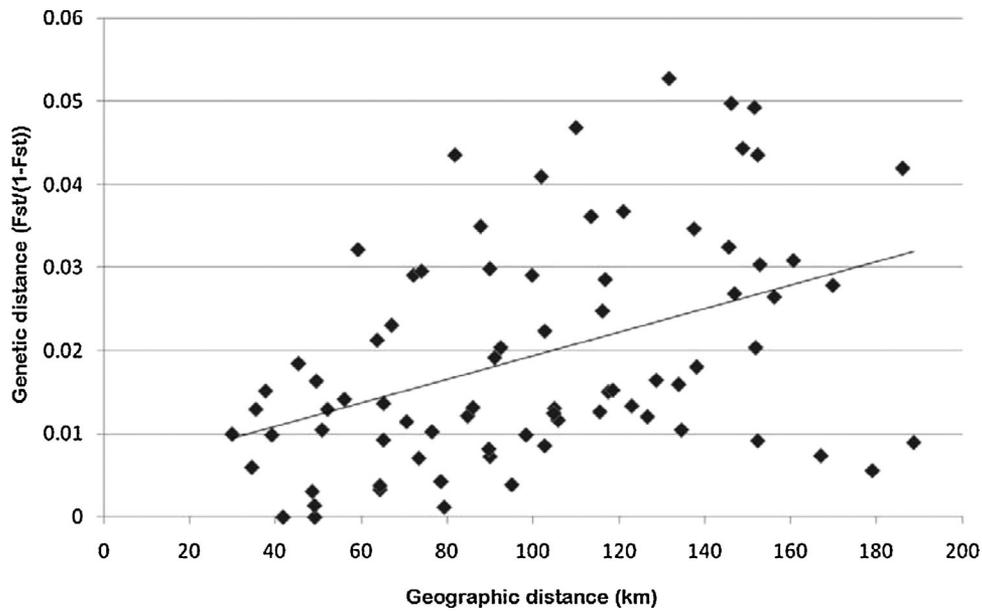


Figure 2. Analysis of isolation by distance showing the relationship between inter-group genetic differentiation as a function of distance ($R^2 = 0.186$; $P < 0.05$) for white-tailed deer in southern Michigan (USA) harvested between 1998–2000.

example, groups located in the center of the study area inhabiting areas of generally poorer habitat (groups 12 and 13) and peripheral groups with comparatively higher HSI (e.g., groups 1 and 11) were characterized by lower and less variable inter-group F_{st} values (Fig. 4).

Effects of the Landscape Matrix on Spatial Genetic Structure

Four landscape features explained more of the variability in genetic differentiation among groups, as indicated by a higher r^2 value than Euclidean distance alone. The high-traffic highway (i.e., Interstate highway 75), rivers, and intermediate habitat suitability appeared to act as barriers to gene flow, and the cost values maximizing r^2 for these

features were 10,000, 1,000, and 100, respectively (Table 3). Low habitat suitability facilitated gene flow; the cost value that maximized r^2 was less than 1 (estimated resistance weight 0.1). Medium- and low-traffic highways and areas classified as high habitat suitability did not explain more of the variation in genetic differentiation than Euclidean distance alone, and thus we did not include them in final resistance surfaces to explain SGS.

The Mantel and partial Mantel tests indicated that the best models for explaining genetic differentiation included rivers, intermediate habitat suitability, and low habitat suitability (Table 4). However, the confidence intervals for

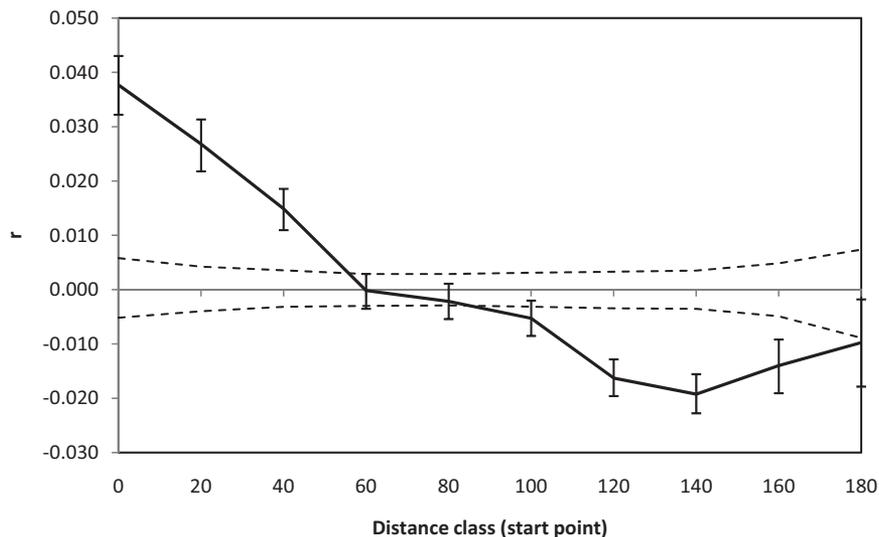


Figure 3. Correlograms of correlation coefficients (r) of geographic and genetic distance at variable distance classes (km) for individual white-tailed deer harvested in southern Michigan, USA (1998–2000). Upper and lower error bars are bound by 95% confidence intervals around each r , and dashed lines indicated 95% confidence limits (upper [U] and lower [L]) around the null hypothesis of a random spatial distribution of genotypes.

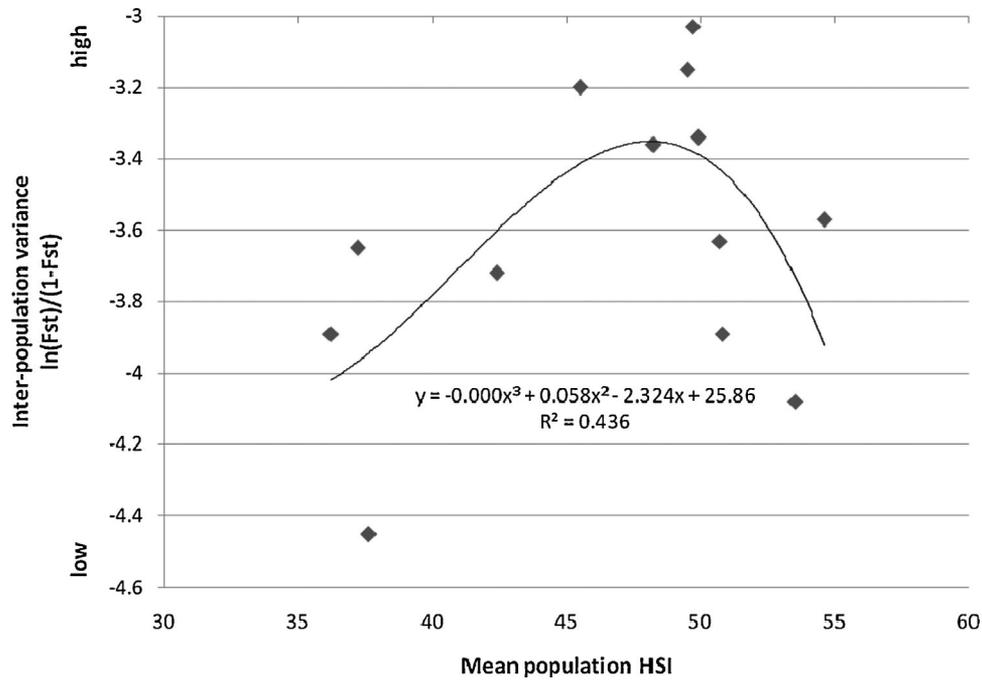


Figure 4. Graphical relationship between mean genetic differentiation (natural log of point estimates over all pairwise comparisons) between groups of white-tailed deer harvested in southern Michigan, USA (1998–2000) and average habitat suitability index (HSI) estimates for the sampling area encompassing each white-tailed deer group.

the cost value (cost = 100) maximizing r^2 ($r^2 = 0.555$, lower = 0.33, upper = 0.71) for intermediate habitat suitability overlapped the confidence limits for the r^2 value at a cost of 0.1, thus suggesting that the inhibiting relationship to genetic differentiation may be weak (Table 3). Likewise, the confidence limits for the cost value (cost = 0.1) maximizing r^2 ($r^2 = 0.430$, lower = 0.31, upper = 0.57) for

low habitat suitability overlapped that of the r^2 value for a cost of 10, thus suggesting that the facilitating relationship to genetic differentiation may be weak (Table 4). The second-best model according to the Mantel and partial Mantel tests included the high-traffic highway and rivers. The lower confidence limit of the maximum r^2 value for the high-traffic highway was greater than the upper limit for

Table 3. Estimates of r^2 from Mantel tests among measures of inter-group genetic differentiation [$F_{st}/(1 - F_{st})$] between groups of white-tailed deer harvested in southern Michigan, USA (1998–2000) and each of several landscape features assessed at each of several resistance values. Values with a dagger (†) indicate features and costs that improved model predictability over Euclidean distance alone ($r^2 = 0.381$). Upper and lower 95% confidence limits are given in parentheses below significant cost values ($P < 0.05$) with higher r^2 values than Euclidean distance. Hwy, highway; HSI, habitat suitability index.

	Cost values							
	Facilitate gene flow				Inhibit gene flow			
	0.0001	0.001	0.01	0.1	10	100	1,000	10,000
All hwy (same weights)	0.375	0.375	0.243	0.241	0.375	0.369	0.226	0.151
High traffic hwy (I-75)†	0.213	0.213*	0.216* (0.13–0.34) ^l	0.243*	0.382*	0.424*	0.593*	0.631†*
Medium traffic hwy	0.175	0.176	0.182	0.239	0.381	0.341	0.131	–0.138
Low traffic hwy	0.231	0.254	0.297	0.318	0.381	0.375	0.319	0.237
Rivers†	–0.133	–0.133	–0.125	0.000	0.378* (0.26–0.51)	0.372* (0.27–0.52)	0.396†* (0.25–0.49)	0.382
High HSI	–0.013	0.02	0.031	0.111	0.361	0.326	0.029	–0.125
Intermediate HSI†	–0.147	–0.101	0.043	0.326*	0.399*	0.555†*	0.547*	0.506*
Low HSI†	0.307	0.294	0.32	0.430†* (0.31–0.57) ^l	0.352* (0.23–0.49) ^l	–0.057	–0.168	–0.143
Euclidean distance		0.381 (0.27–0.51)						

* Indicates significant cost values ($P < 0.05$).

Table 4. Correlation coefficients, lower and upper confidence limits from Mantel and partial Mantel tests on the relationship between resistance surfaces containing various landscape features and spatial genetic structure [$F_{st}/(1 - F_{st})$] among white-tailed deer groups in southern Michigan, 1998–2000. Hwy, high traffic highway (Interstate highway I-75); HSI, habitat suitability index; EucDist, Euclidean distance.

Features	Mantel			Partial Mantel		
	r^2	Lower	Upper	r^2	Lower	Upper
River, medium_HSI, low_HSI	0.712	0.629	0.793	0.652	0.563	0.731
Hwy, river	0.673	0.521	0.833	0.602	0.418	0.788
Medium_HSI, low_HSI	0.652	0.509	0.774	0.584	0.41	0.722
River, medium_HSI	0.639	0.541	0.763	0.586	0.466	0.719
Hwy, river, low_HSI	0.632	0.477	0.805	0.554	0.383	0.76
Hwy, river, medium_HSI	0.629	0.495	0.841	0.544	0.399	0.783
Hwy, river, medium_HSI, low_HSI	0.626	0.485	0.831	0.546	0.395	0.777
Hwy, low_HSI	0.624	0.464	0.813	0.544	0.36	0.757
Hwy, medium_HSI	0.615	0.469	0.829	0.528	0.352	0.77
EucDist	0.381	0.266	0.513			

cost values <1 . For rivers, cost values <1 were not significant. Thus, the presence or absence of rivers in the landscape matrix between populations was predictive of inter-group F_{st} ($r^2 = 0.396$) and significantly exceeded relationships based on Euclidean distance alone ($r^2 = 0.381$; Table 3). The strongest inhibitor of gene flow (i.e., significant improvement over the model with Euclidean distance alone) was when we conducted the cost analysis using the high-traffic highway (i.e., Interstate highway 75; Fig. 1) that separates groups 9 through 11 from the rest of the study area. This highway also separated the majority of members of the 2 inferred genetic clusters (see above; Fig. 1).

According to AIC, the final model of best fit included the high-traffic highway, rivers, intermediate habitat suitability, and Euclidean Distance (AIC = -704.7 , $r^2 = 0.426$; Table 5), and also explained more of the variation in genetic differentiation than Euclidean distance alone ($r^2 = 0.186$). The second best model contained the high-traffic highway

and rivers ($r^2 = 0.384$) and also explained more of the genetic variation than Euclidean distance alone. Permutation testing revealed that these relationships did not occur by random chance ($P < 0.001$). Final model averaged parameter estimates were $\hat{\beta}_0 = 0.004$ (SE = 0.003), $\hat{\beta}_1 = 2.65E - 9$ (SE = $7.01E - 10$), $\hat{\beta}_2 = 1.60E - 7$ (SE = $5.13E - 8$), $\hat{\beta}_3 = 7.39E - 8$ (SE = $4.12E - 8$), $\hat{\beta}_4 = 2.29E - 7$ (SE = $1.01E - 7$) for high traffic highways, rivers, medium HSI, and Euclidean distance, respectively (Table 5).

DISCUSSION

Evaluation of landscape features associated with connectivity between patches has wide applications in wildlife conservation planning at multiple spatial scales (Calabrese and Fagan 2004, Urban et al. 2009). We developed a connectivity model for white-tailed deer and evaluated multiple least cost models to measure associations between landscape features and measures of genetic diversity within and among deer groups

Table 5. Akaike's Information Criterion (AIC), relative AIC (ΔAIC) values, model likelihood, and Akaike weights (wt) for various models explaining spatial genetic structure [$F_{st}/(1 - F_{st})$] among white-tailed deer groups in southern Michigan, 1998–2000. Hwy, high traffic highway (Interstate highway I-75); Low_HSI, low habitat suitability; Med_HSI, medium habitat suitability; Hi_HSI, high habitat suitability; EucDist, Euclidean distance.

Parameter	R^2	AIC	ΔAIC	Likelihood	Akaike wt
Hwy, river, med_HSI, EucDist	0.426	-704.7	0	1.00	0.47
Hwy, river	0.384	-703.2	1.5	0.47	0.22
Hwy, river, low_HSI	0.387	-701.6	3.1	0.21	0.10
Hwy, river, med_HSI	0.385	-701.4	3.3	0.19	0.09
Hwy, river, low_HSI, med_HSI	0.393	-700.4	4.3	0.12	0.06
Hwy, med_HSI	0.347	-698.7	6.0	0.05	0.02
Hwy, low_HSI	0.342	-698.1	6.6	0.04	0.02
Hwy, low_HSI, med_HSI	0.351	-697.1	7.6	0.02	0.01
Hwy	0.297	-694.9	9.8	0.01	0.00
River, med_HSI	0.270	-690.0	14.7	0.00	0.00
Med_HSI	0.244	-689.2	15.5	0.00	0.00
Low_HSI, med_HSI	0.270	-688.2	16.5	0.00	0.00
River, low_HSI, med_HSI	0.253	-688.0	16.7	0.00	0.00
Low_HSI	0.239	-687.0	17.7	0.00	0.00
River, low_HSI	0.222	-686.8	17.9	0.00	0.00
River	0.220	-686.8	17.9	0.00	0.00
EucDist	0.186	-683.6	21.1	0.00	0.00

in southern Michigan. Our global analysis using multiple methods (Mantel tests and AIC model evaluation) to quantify effects of factors influencing SGS provided evidence that landscape features between groups, such as rivers and high-traffic highways, were barriers to movement and were significant predictors of SGS (Tables 3 and 5). Natural landscape features such as rivers have previously been documented as imposing a barrier to white-tailed deer gene flow (Blanchong et al. 2008, Robinson et al. 2012). Man-made features of more recent (<65 years) origin such as highways were also found to inhibit gene flow (Long et al. 2010) although white-tailed deer adapt well to urbanization and fragmentation (Ditchkoff et al. 2006). The largest (highest traffic volume) and oldest highway (Interstate highway 75 in the eastern portion of the study area constructed in the mid 1950–1960s) represented a significant impediment to gene flow (Table 3), and coincided with the boundaries of the 2 genetic clusters (Fig. 1). Roads have frequently been shown to have negative effects on wildlife movement (Foreman and Alexander 1998, Trombulak and Frissell 2000, Underhill and Angold 2000, Balkenhol and Waits 2009). With increasing human populations, transportation networks and highway traffic volume are likely to increase with expansion of urban and suburban areas (Borda-de-Aqua et al. 2011). Given the relationships between SGS and presence of roads for highly vagile white-tailed deer, spatial genetic structure of species with lower vagility and lower variance effective population size would be expected to be more dramatically affected by anthropogenic disturbance.

Interpreting results from statistical tests of spatially distributed phenomena is challenging because of issues with spatial autocorrelation and strengths and weaknesses of each test. For instance, partial Mantel tests and their associated analyses (e.g., Multiple Regression on Distance Matrices, MRM) have high type 1 error rates (Balkenhol et al. 2009, Legendre and Fortin 2010), and information theoretic approaches assume data independence (Burnham and Anderson 2002). However, landscape genetic studies commonly employ a number of analytical methods, and the challenge is then to interpret several different model results while taking into account the limitations of the approaches. Both of our modeling approaches converge on the results that rivers and high-traffic highways were significant predictors of SGS. The relationship between genetic diversity and landscape-level habitat suitability metrics was less obvious. However, measures of habitat quality quantified within and between areas occupied by deer groups were also associated with SGS, as exemplified by regression analysis of HSI for sampling areas encompassing white-tailed deer groups and F_{st} (Fig. 4) and the results of Mantel tests (Table 3), but to a lesser degree than rivers and the high-traffic highway. For example, groups collected from areas where habitat was of intermediate quality were more highly differentiated from deer in other groups relative to deer collected from areas of high and low habitat quality (Fig. 4). Thus, the permeability of intermediate quality habitat may be lower, meaning these areas inhibit gene flow,

whereas areas of low habitat suitability may facilitate gene flow (Tables 3 and 5). In addition to the comparison of mean genetic differentiation and HSI, model selection based on AIC suggested that intermediate habitat suitability (inhibitor) and low habitat suitability (facilitator) were significantly better predictors of genetic differentiation than Euclidean distance alone. Although the Mantel tests suggested these habitat relationships may not be significant (Table 3), the partial Mantel test and model selection based on AIC alluded to their significance (Tables 4 and 5). Alternatively, the habitat classes may not correctly reflect permeability or gene flow, or may not be sufficient to detect patterns at the scale of analysis. For instance, the variability in HSI is diluted as scale becomes coarser. The variation in significance of habitat suitability with different analysis methods warrants further investigation of the effects of habitat on spatial genetic structure at large landscape scales.

One important assumption underlying the approaches used in this study, and those commonly used in landscape genetic analyses (Hall and Beissinger 2014), is that the relationships of interest are stationary or homogeneous spatially. The non-random distributions of habitats of comparatively higher and lower quality across the study area (Fig. 1) and the prominent effects of interstate highway 75 on SGS (i.e., based on the abrupt discontinuity in genetic cluster; Fig. 1) suggests non-stationarity of effects of landscape features and barriers affecting SGS. Alternative analytical methods such as geographically weighted regression (GWR; Fotheringham et al. 2002) can account for spatial components of the data including local regression. However, GWR analyses requires large datasets (ideally at least 40 measurements in weighted regressions for each set of points (distance intervals; Fotheringham et al. 2012), and for this reason, GWR has not often been applied in landscape genetic studies. Across our study area, the number of groups and inter-group comparisons within and between patches were not sufficient to use this approach. Other approaches such as multiple regression on distance matrices (MRM; Lichstein 2007) would allow the examination of how landscape features affect patterns of genetic variance at varying distances; however, the restricted number of groups precluded use of this or other similar approaches.

The low inter-group genetic differentiation in groups of deer inhabiting lower quality habitats may be due to lower deer density in these areas, especially if the low suitability areas were isolated or surrounded by intermediate habitat quality, which may inhibit gene flow (Table 3). For example, Roseberry and Woolf (1998) reported a positive curvilinear relationship between white-tailed deer densities and habitat suitability in an agricultural region in the mid-western United States similar to our study area. Genetic differentiation may be low in areas of higher quality habitat if deer were able to meet life requisites and therefore, were less likely to disperse (King 1938, Clobert et al. 2004), particularly if immigration into these areas was also concurrently low. For instance, Felix et al. (2007) found that non-migratory deer in Michigan occupied areas of comparatively higher quality winter and summer habitat than migratory deer that

occupied areas where at least 1 critical habitat component was missing from their seasonal home range. Deer in Pennsylvania dispersed greater distances in areas with less forest cover, which was related to lower habitat quality (Long et al. 2005). Social organization of white-tailed deer (i.e., differences in degree of male and female philopatry) may also explain SGS (Chesser 1991, Scribner et al. 2001). To substantiate these hypotheses, future research should investigate the interrelationships among habitat suitability, deer densities, movement patterns including dispersal and migration, social organization, and SGS.

Evidence for multi-generational or long-distance dispersal in our study is based on the dispersion of individuals with high posterior probabilities of affiliation with the genetic cluster whose members are predominately found in the eastern portion of the study area (Fig. 1) and the significance associated between inter-group genetic differentiation and geographic distance across the entire study area (Fig. 2). Although the effects of habitat suitability on long-distance movements are unknown, long-distance movement of white-tailed deer does occur. For instance, in our study area, distances up to 60 km approximates the extent of detectable positive genetic structure. In upper Michigan, seasonal movements of greater than 50 km have been documented (Verme 1973). Although the presence of the highway likely impedes movement, underpasses and natural drainages or waterways may facilitate deer passage in some instances (Donaldson 2007, Corlatti et al. 2009, Ford et al. 2009).

Although quantitative data pertaining to population density are not available, density certainly varies across the large southern Michigan study area and throughout the course of a year and could affect interpretations of results. Spatial and temporal variability in deer density is likely due in part to habitat quality and thus we expected collinearity between site- (or group-) specific density and habitat quality. For example, Roseberry and Woolf (1998) found that 81% of the variation in local deer density was attributed to habitat quality. Density likely also varies spatially and temporally in a sex-specific manner (Bowyer 2004). Dispersal, migration, and human activities such as baiting during hunting season would also affect densities in localized areas as well as SGS (Blanchong et al. 2006). Samples were collected during the annual firearms harvest period but no data are available on hunter effort or method of harvest. Movements of deer and changes in local densities throughout the course of the year may be a source of variability in our data. However, the fact that the results showed relationships between measures of SGS, barriers, and HSI in the absence of information on variation in density suggests the results are likely robust.

Our analyses relied on measures of potential resistance of landscape features to deer gene flow. Development of predictive measures of resistance is challenging. Dispersal is frequently conditional upon resource availability (e.g., food, access to mates), and population density (Ronce et al. 2001, Clobert et al. 2009), which vary spatially and temporally. Resource availability can be estimated with measures of habitat suitability, which are generalized estimates not reflecting inherent variation at the microhabitat scale or may

vary because of factors such as drought, flooding, crop rotations, or other events. Spatial and temporal scales over which samples are collected (Anderson et al. 2010) and cost surfaces (Spear et al. 2010) associated with landscape features should be considered in experimental designs. Our estimates of habitat suitability were based on data independent of this study using telemetry data on deer in several portions of our study area in southern Michigan (Pusateri 2003, Hiller 2007). Generalizations of the relative effects of habitat features on SGS documented in Michigan to other areas of the species range will require additional study.

Weighting of landscape features for the development of the least cost distances is based on perceived measures of permeability. Relative cost values assigned to different landscape features are usually arbitrary because the true cost to wildlife is unknown (Pérez-Espona et al. 2008). The cost value assigned to each landscape feature will also affect the modeled relationship between genetic structure and landscape features (Spear et al. 2010, Manel and Holderegger 2013). Our approach of evaluating model fit using a range of cost values for each feature and identifying the weighting value that improved model fit associated with variation in the relationship between genetic structure and landscape features explicitly addresses the question of uncertainty in a systematic manner, and allowed us to identify relative influences of landscape features on genetic structure of white-tailed deer in Michigan.

MANAGEMENT IMPLICATIONS

Evaluating impacts of anthropogenic activities on natural systems is becoming increasingly critical as human populations are expanding and affecting animal movements and habitat occupancy. Studies documenting the effects of landscape features on gene flow in highly mobile species of conservation and management interest are limited, particularly in human-altered landscapes. The relative impacts of natural and man-made landscape features on gene flow in white-tailed deer speak to the importance of joint ecological and genetic analyses in present and future conservation efforts of landscapes and wildlife species using them. We quantified the importance of roads and rivers on gene flow of white-tailed deer. Based on our data, these predominant features of human-modified landscapes are barriers to gene flow and can be used in delineating management units and to direct efforts to control immigration into and emigration from areas bounded by these major barriers. Future studies quantifying the influence of landscape features on wildlife, both within and between locales will help managers and planners design landscapes to meet human needs while understanding potential implications of anthropogenic activities on wildlife.

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