



DECEMBER 2014

How Does Landscape Affect Northern Bobwhites?

Katherine S. Miller, Ph.D.

This project spanned a large area, from Texas into the Great Plains. Balancing field sampling with laboratory research and coursework would have been daunting without the hunters and state biologists who mailed in hunter-harvested wings, saving me travel and time. I was also fortunate to work with researchers in their fields of quail, Dr. Brennan and Dr. Hernandez, molecular ecology, Dr. DeYoung, and landscape ecology, Dr. Wu. I was funded by the Elliot and Adelle Bottom Fellowship in Quail Research, Quail Associates, the South Texas Chapter of the Quail Coalition, Amanda Whitaker Memorial Scholarship in Quail Research, and the Phil M. Plant scholarship. This project would not have been possible without your assistance. Thank you!

INTRODUCTION

Northern bobwhite populations have declined in the last 50 years (Sauer et al. 2012), primarily due to loss of habitat through fragmentation. For a short-distance disperser, like quail (Leopold 1933), one would expect moderate genetic structure among populations. However, previous genetic studies on northern bobwhite at Caesar Kleberg Wildlife Research Institute (Wehland 2006, Williford et al. 2014) revealed high genetic diversity and weak genetic structure among northern bobwhite populations. Some birds travel long distances, sometimes more than 16 km (Lehmann 1984, DeMaso et al. 1997). Therefore, dispersal may be more important for northern bobwhite populations than biologists initially thought. Fragmentation of the habitat may disrupt the connectivity, and gene flow, among northern bobwhite populations. Biologists have called for management at the landscape level to halt or reverse population declines in grassland bird species (Williams et al. 2004, Brennan and Kuvlesky 2005, Hernández et al. 2013).

My goal was to use causal modeling to investigate effects of barriers and landscape features on gene flow and population structure of northern bobwhites in Texas and the Great Plains.

METHODS

The scope of this research spanned a large geographic area (1,359,412 km²), and spanned different habitats: grasslands and thorn-scrub in southern Texas (Hernández et al. 2007, Rader et al. 2007), tall grass prairie in the Great Plains of Kansas (Caire et al. 1989), and east to western Missouri and southern Iowa (Figure 1).

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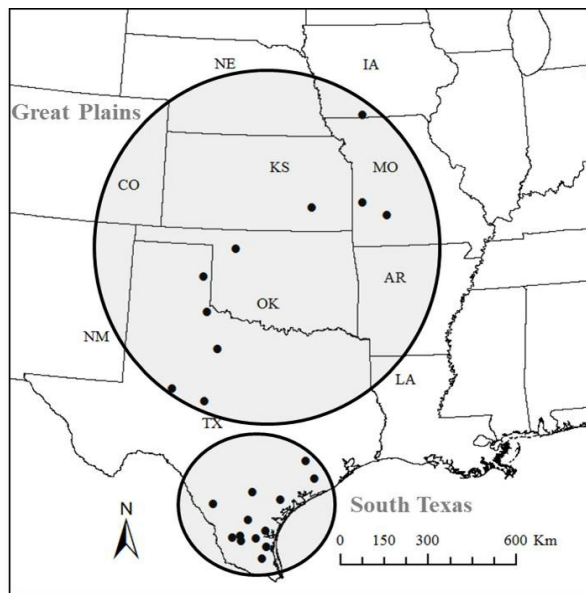


Figure 1 Sample locations for northern bobwhite (*Colinus virginianus*), 2010–2013 (spanning 3 hunting seasons). Locations were grouped into 2 regional areas, Great Plains and South Texas.

I removed a small sample of tissue (wings) or calamus (feathers), and extracted the DNA. I used 13 microsatellite DNA loci (Schable et al. 2004, Faircloth et al. 2009) to determine genetic diversity (allelic richness, Kalinowski 2005; heterozygosity, Excoffier and Lischer 2010) and population structure (Analysis of Molecular Variance, AMOVA, Weir and Cockerham 1984, Excoffier et al. 1992; F_{ST} , Weir and Cockerham 1984).

I quantified genetic distance among populations using pairwise genetic distance (D_{est} , Jost 2008). I developed 7 models (Figure 2) to assess the effects of geographic distance, barriers, or resistance in the landscape on population structure of northern bobwhites. Barriers included highway interstates and major rivers (Figure 3). Three models tested single effects of isolation by distance, barrier, and landscape resistance. I used the National Bobwhite Conservation Initiative's (NBCI) landcover map (Terhune and Palmer 2011) to develop 7 alternative landscape resistance maps (Figure 4, Cushman et al. 2006, Spear et al. 2010). Landscape resistance surfaces use values that represent the degree to which the features impede movement (Spear et al. 2010). Populations of northern bobwhite may be affected by multiple factors, so I tested 4 more models that combined isolation by distance and barrier, distance and resistance, barrier and resistance, and all three factors. I used partial Mantel tests to measure the relationship between genetic distance and an effect (distance, barrier, landscape resistance), accounting for another effect, among the sampled populations (Mantel 1967, Cushman et al. 2006). I then compared the observed correlation coefficients and P values (10,000 permutations) with the expectations of the 7 models. Results are presented as $\pm SE$ unless otherwise noted.

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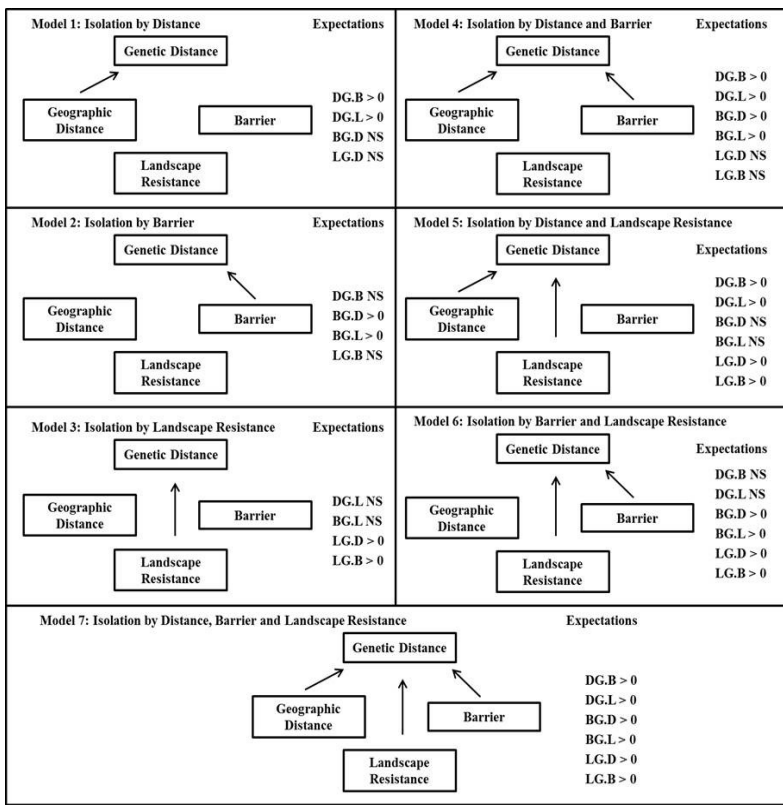


Figure 2. Causal models, developed to assess the effects of landscape features on genetic differentiation of northern bobwhite (*Colinus virginianus*) populations in Texas and the Great Plains (following Cushman et al. 2006). Distance (D) is the Euclidean distance between two populations. Barrier (B) includes interstates and major rivers. Landscape resistance (L) refers to 7 maps of varying resistances to northern bobwhite movement, using the National Bobwhite Conservation Initiative's (Terhune and Palmer 2011) habitat raster. The notation DG.B refers to the partial Mantel test where the correlation between D and G is estimated after the effects of B are partialled out.

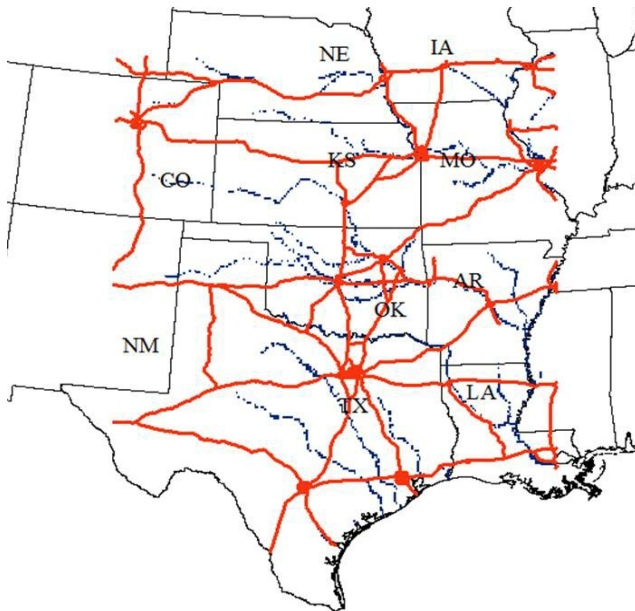


Figure 3. Potential barriers to dispersal for northern bobwhites (*Colinus virginianus*) include interstate highways (red) and major rivers (blue).

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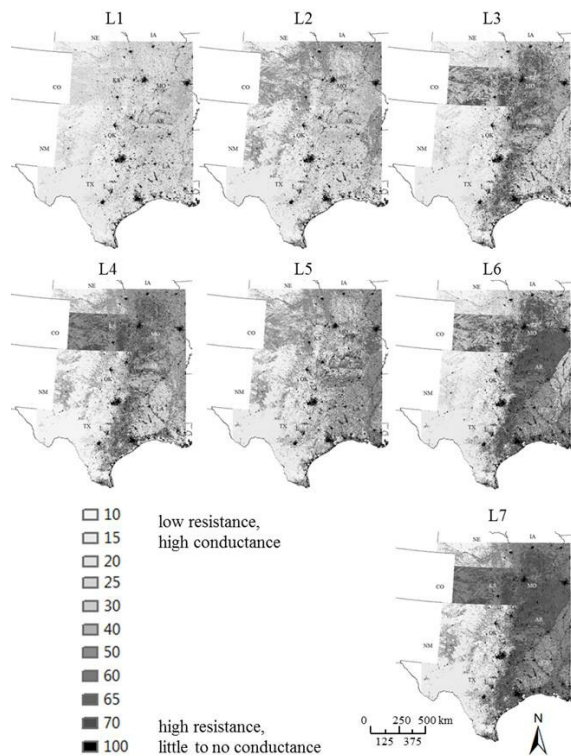


Figure 4. Hypothesized landscape resistance maps for northern bobwhite (*Colinus virginianus*), based on the National Bobwhite Conservation Initiative's landcover raster (Terhune and Palmer 2011). L1–L4 assumed moderate resistance in woodlands. L1 assumed idle pasture, improved (small fields, hedgerows) farming, L2 idle pasture, clean farming, L3 unsuitable (too woody, or overgrazed) pasture, small field agriculture, and L4 unsuitable pasture, clean farming. L5–L7 assumed higher resistance in woodlands. L5 assumed idle pasture, clean farming, L6 unsuitable pasture, small field agriculture, and L7 unsuitable pasture, clean farming.

RESULTS

I extracted usable DNA from 641 birds representing 23 populations. Ten populations were in the Great Plains group and 13 populations were located in the South Texas group. Samples from 1 area in east Texas, 2 areas in Oklahoma, 1 area in Kansas, and 3 areas in northern Missouri did not amplify sufficiently for analyses.

Allelic richness and heterozygosity reflected moderate genetic diversity in all the northern bobwhite populations. Allelic richness did not differ significantly between regions (Great Plains region, 4.86 ± 0.04 ; South Texas, 4.68 ± 0.05 ; $t_{21} = 1.64$, $P = 0.12$). Heterozygosity did not differ between the Great Plains and South Texas (0.63 ± 0.01) regions. Over the sampling area, the population genetic structure was weak ($F_{ST} = 0.023$, $P < 0.001$). The AMOVA partitioned most genetic variation within the populations (97.6%) rather than among regions or among populations within regions. Average genetic distance (D_{est}) among populations was weak (0.031 ± 0.002 , $0-0.130$, $n = 253$ pairs).

Overall, the tests met all the assumptions of the barrier model (Figure 5a). In the Great Plains region, the tests met all the assumptions of the isolation by distance model (Figure 5b). The tests in South Texas met the landscape resistance model (3 out of 4 models, Figure 5c). The strongest correlations occurred when pasture resistance was set low, and agriculture resistance was set moderately high.

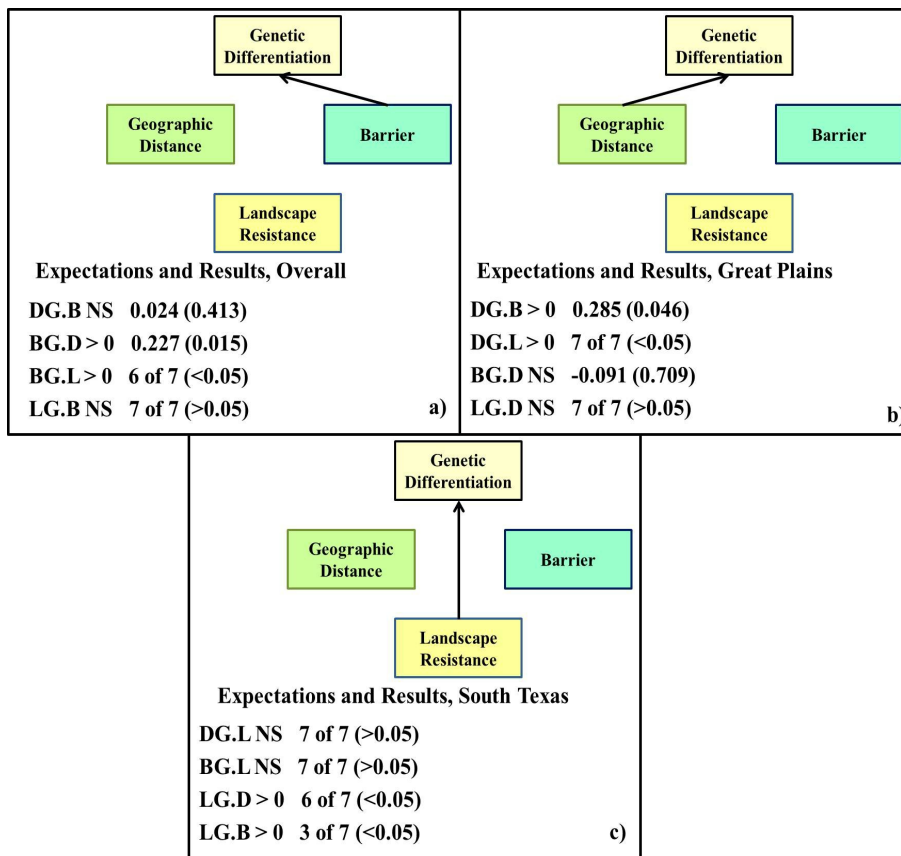


Figure 5 Expectations of a) barrier model and results, overall, b) distance model and results, Great Plains, and c) landscape resistance and results, South Texas. Partial Mantel correlations shown for distance and genetic differentiation, with barrier partialled out, and barrier and genetic differentiation, with distance partialled out, with *P* value in parentheses. For landscape tests, *P* value from partial Mantel test is shown in parentheses.

DISCUSSION

If northern bobwhites make short dispersals, as most telemetry studies suggest, then limited gene flow among populations should result in isolation of populations, low genetic diversity, and moderate structure among populations (Murphy et al. 2010, Klicka et al. 2011). In contrast, northern bobwhite populations in this study displayed weak genetic structure over a broad geographic area and similar levels of genetic diversity, consistent with previous studies (Eo et al. 2010, Williford et al. 2010, Berkman et al. 2013).

Although population structure was low, I detected subtle effects of landscape features on genetic differentiation. Populations in the Great Plains were isolated by distance, unlike populations in South Texas. Isolation by distance is expected for a short-distance disperser like northern bobwhite. The distance effect in the Great Plains but not in South Texas may be due to the larger geographic scale of sampling in the Great Plains, or may also have to do with differences in continuity of the landscape among the 2 regions. Interstates and major rivers were the most important isolating factor for the overall model, despite the weak genetic structure. In the Great Plains region, northern bobwhites mostly exist in patches of habitats isolated by roads, rivers, and patches of unsuitable habitat. Northern bobwhites might cross these barriers to habitat patches successfully at times, but an accumulation of highways and rivers can become barriers to gene flow. Isolation by landscape resistance was expected for northern bobwhite in the overall model, yet only the populations in South Texas appeared to be affected by the landscape. This may be due to the difference in spatial scale as well.

The weak population structure and overall genetic similarity over the broad geographic scale of this study was unexpected. This may have been influenced by sampling limitations or northern bobwhite behavior. Northern bobwhites were harvested by hunters from relatively abundant populations, while small populations in more isolated areas were less likely to be hunted. Sampling

considerations cannot account for the overall genetic similarity over the entire region, however. Northern bobwhites undergo a “fall shuffle” (Lehmann 1984), which may affect the distribution of alleles, and thus the genetic diversity in the population. Weak genetic structure of northern bobwhite populations may also be due to their breeding system. Females will often lay a second clutch if the first nest fails, and sometimes even if the first nest is successful. A different male may sire the second clutch (Taylor 1991, Curtis et al. 1993). Extra-pair fertilization may also occur in northern bobwhite populations (Burger et al. 2005, Brennan et al. 2014). It seems possible that for northern bobwhite populations, polygamy, covey shuffles, and both short-distance and long-distance dispersals may act together to the extent that low genetic structure is maintained.

Management Implications

Landscape alteration can eventually result in the local or regional extirpation of northern bobwhites. Nonetheless, my results suggest that the behavior and population dynamics of northern bobwhite in Texas and the Great Plains may drive sufficient effective population size or gene flow to limit the loss of genetic diversity in the fragmented landscapes. Once the effective population size goes below an unknown level, there may be a tipping point, where populations are prone to collapse. Therefore, the quantity and quality of habitat should remain a focus for management in fragmented landscapes.

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CHANGING TIMES!

I have enjoyed compiling these newsletters, but the time has come to pass the reins! Casey Cain, a native of Nebraska and a Ph.D student with Dr. Brennan, will be assuming all Quail Associate and Quail eNews duties effective January 1st, 2015. You can reach Casey Cain at casey.cain@students.tamuk.edu. I hope to see some of you at upcoming conferences!

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