Population Genomic Analyses Separate Historic Translocations from Contemporary Gene Flow in Arkansas White-tailed Deer (*Odocoileus virginianus*)

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ABSTRACT

Approximately 100 years ago, hunter-harvest eliminated white-tailed deer (WTD; *Odocoileus virginianus*) in eastern North America, which subsequently served as a catalyst for wildlife management as a national priority. An extensive stock-replenishment effort soon followed, with WTD broadly translocated among states as a means of reestablishment. Now, contemporary issues focus on reverberations from a global (and fatal) epizootic disease in Cervidae (chronic wasting disease, CWD). These cumulative impacts have effectively obscured the traditional signals of post-translocation gene flow and dispersal in North American WTD. To develop baseline data for its adjudication, we applied cutting-edge molecular and biogeographic tools to process 1,143 WTD sampled state-wide in AR, with 54,102 single nucleotide polymorphisms (SNPs) derived via reduced-representation genomic sequencing. We then employed Simpson's diversity index to visualize landscape genetic patterns previously obscured by extensive translocations, and this allowed us to summarize multidimensional ancestry assignments and identify spatio-genetic transitions. We then sub-sampled transects and tested clinal patterns across loci for concordance and/or coincidence. Two salient results emerged: (A) Genetic echoes from historic translocations are widely apparent; and (B) Geographic filters (major rivers; urban centers; highways) now act as inflection points for the distribution of more contemporary ancestry. These results, in synergy, yielded a state-wide assessment of how historic translocations, as well as ongoing processes, have acted to dictate contemporary population structure of Arkansas WTD. In addition, the analytical framework employed herein effectively deciphered the extant/historic drivers of WTD distribution in AR. It is also applicable for other biodiversity elements with demographic histories equally as complex.

1 | INTRODUCTION

Distribution and abundance are key natural history attributes that provide a foundation for organismal ecology (Andrewartha & Birch, 1956; Kissling et al., 2018). Each is geographically and hierarchically structured, often across several spatial scales, and in response to a non-random distribution of resources and refugia (Turner, 1989). Species distributions and abundances are increasingly impacted by habitat fragmentation, over-exploitation, and translocation in the Anthropocene (Baker et al., 2017; Corlett, 2015), with the functional integrity of these attributes being severely challenged. Hunter-harvest, an additional anthropogenic impact, also exerts a relatively consistent global impact on biodiversity (Darimont et al., 2009). Given the manner by which abundances and distributions have been so impacted, other attributes such as dispersal and population connectivity have subsequently emerged as focal points for contemporary wildlife management, (Crooks & Sanjayan, 2006; Cushman, Elliot, Macdonald, & Loveridge, 2016). Here we focus on these latter attributes as we evaluate historic and contemporary population structure in a wild Arkansas (AR) ungulate (white-tailed deer, WTD; *Odocoileus virginianus*).

1.1 | Dispersal, connectivity, and population structure

Dispersal and connectivity have been traditionally assayed for management purposes using direct methods such as radio- and satellite-tracking (Kays, Crofoot, Jetz, & Wikelski, 2015), yet both have deficiencies such as low sample-sizes and a perspective that must extrapolate from individuals to populations (Katzner & Arlettaz, 2020). An indirect approach, on the other hand, relies instead upon gene flow (i.e., movements, demographics) and genetic drift (i.e., heterozygosity, effective population size) to quantify population-level movement ecology captured over many generations (Bossart & Prowell, 1998; Comte & Olden, 2018). Landscape

genetics, for example (Richardson, Brady, Wang, & Spear, 2016), quantifies movement patterns by evaluating the spatial structure inherent to genetic diversity (as mediated by dispersal and gene flow), and does so for greater numbers at a fraction of the per-individual cost (Picard et al., 2017; van Rees, Reed, Wilson, Underwood, & Sonsthagen, 2018; Wang & Shaffer, 2017).

We now recognize that genotypes within a species (i.e. gene pool) vary across landscapes, often coalescing as discretely recognizable sub-populations (i.e., intra-specific population structure driven by mutation, selection, gene flow, genetic drift), and visualized/ interpreted at varying degrees both temporally and spatially (Barton & Clark, 1990; Slatkin, 1989). They span from the afore-mentioned sub-populations through continuously decreasing gradients of genetic similarity that extend over geographic or environmental distance (i.e., isolation by distance: Avise 1992; Bohonak 1999; Bradburd et al. 2018). Structure can be ascertained by sampling individuals across appropriate spatial scales, relative to the dispersal kernel of the organism (Nathan, Klein, Robledo-Arnuncio, & Revilla, 2012). It can then be employed to test hypotheses about the likely causes of observed genetic patterns (Bradburd, Ralph, & Coop, 2016; Miles, Rivkin, Johnson, Munshi-South, & Verrelli, 2019). However, gene flow and genetic drift are often conflated, and their deconstruction is an important aspect when attempting to clarify how population genetic structure is driven.

Patterns of genetic diversity are also impacted by multiple extrinsic and intrinsic factors. For WTD, those extrinsic may include: Rivers, interstate highways, large tracks of forested habitat (Robinson, Samuel, Lopez, & Shelton, 2012); agricultural land use, climate-related factors (Brinkman, Deperno, Jenks, Haroldson, & Osborn, 2005); and landscape connectivity (Koen, Tosa, Nielsen, & Schauber, 2017). Intrinsic factors, on the other hand, may reflect: Population density (Lutz, Diefenbach, & Rosenberry, 2015); age structure/ sex ratio (Long,

Diefenbach, Rosenberry, & Wallingford, 2008); and social hierarchy (Nixon & Mankin, 2016).

Factors that traditionally shape dispersal and genetic diversity within/ across regions can difficult to quantify in that anthropogenic actions such as translocation or trafficking can obscure existing patterns (Brown, Hull, Updike, Fain, & Ernest, 2009; Shephard, Ogden, Tryjanowski, Olsson, & Galbusera, 2013). This is particularly true for WTD, as it is one of the most recreationally important animal species in North America (Knoche & Lupi, 2012), with populations intensely impacted by both hunter harvest and game management (Waller & Alverson, 1997; Wolverton, Kennedy, & Cornelius, 2007). For example, at the beginning of the 20th century, WTD and other heavily hunted species (e.g., wild turkey) saw heavy declines and widespread extirpations. In a census of the north-central United States, Leopold (1931) noted "… some deer" were still extant in southern Missouri at this time, and this dovetails with WTD numbers estimated in Arkansas (~500 scattered across isolated refugia; Holder, 1951). Subsequent AR efforts to bolster resident numbers and re-populate depleted areas involved translocations within-state, as well as importations from out-of-state. Although successful, a result of these efforts is that apparent genetic patterns are likely to be strongly reflective of artificial, rather than natural, movements.

A first step in designating factors that have shaped WTD population structure and dispersal is to estimate that genetic component that remains within AR WTD genomes as a residual of historic translocations and subsequent genetic drift. Perhaps the most pressing need to understand WTD dispersal is the impact these data have with regard to the potential containment and mitigation of a widespread and fatal neurodegenerative disease of cervids (chronic wasting disease; CWD), that has now become a panzootic (Williams and Young 1980; Escobar et al. 2019; Mawdsley 2020). Thus, efforts to contain and mitigate its spread are paramount for

wildlife management, not only in North America but also globally (Leiss et al., 2017).

1.2 | Dispersal, connectivity, and management

An understanding of the manner by which WTD disperse across the landscape has clear management implications. Its landscape movements are many and varied, as driven by habitat quality, climate, and anthropogenic benefits. Region-specific patterns are needed so as to develop broader generalizations regarding species-specific movement ecology (Brinkman et al., 2005).

The goal of our study was to ascertain if signatures of historic translocations are apparent in, and have contributed to, the genetic diversity and structure of Arkansas WTD, and furthermore, if they can indeed be parsed from ongoing gene flow and genetic drift. To do so, we surveyed a broad array of nuclear genomic markers using ddRAD sequencing (Peterson et al., 2012). Our first objective was to characterize respective patterns of anthropogenic translocation and natural re-colonization via refugial populations, and secondarily to seek evidence for geographic barriers throughout the state that seemingly prevent or actively filter WTD dispersal. However, we hypothesized that the former situation would obscure the latter, in that long-range anthropogenically-mediated displacement of individuals violates methodological assumptions that stipulate gene flow as occurring in a spatially consistent manner (Bradburd & Ralph, 2019).

To address this, we repurposed existing formulas that summarized ancestry assignments by reducing their dimensionality, and mitigated methodological artefacts due to translocation (Simpson, 1949). Our result was an interpolated ‘surface’ representing putative intraspecific suture zones. We also wished to define the respective roles played by stochastic and deterministic processes in generating these zones, particularly given historic population

fluctuations and the internal/ external translocations that conflated the demography of AR WTD. To do so, we borrowed components of clinal variation theory so as to hypothesize the manner by which individual loci should transition across these spaces, relative to a genome-wide average (Barton, 1983; Barton & Hewitt, 1985; Endler, 1973; Hewitt, 2001; Polechová & Barton, 2011; Slatkin, 1973).

Although clinal variation is often taken as evidence for selection, genetic drift in concert with spatially variable gene flow can generate patterns in individual loci that mimic those seen in adaptive clines (Vasemägi, 2006). With drift operating alone, allele frequencies at each locus may wander 'upward' or 'downward' across space as a function of the initial allele frequency. Range expansion or dissemination from refugia can also yield a type of 'rolling' founder effect that can mirror a clinal pattern (Excoffier, Foll, & Petit, 2009; Hallatschek & Nelson, 2008; Hewitt, 2000; Keller et al., 2013). Given this, we might predict that multi-locus patterns at intraspecific suture zones generated solely as a result of genetic drift in expanding populations will be dominated by stochastic directional change, with each drifting either up or down with respect to the genome-wide average (Santangelo, Johnson, & Ness, 2018). On the other hand, a strong barrier to movement would yield a discontinuity in the rate of this change across space (Barton, 2008; Nagylaki, 1976; Slatkin, 1973). The existence of a barrier (either impacting dispersal or as a strong fitness differential) thus implies the presence of an inflection point that would induce a sigmoidal change in locus-specific ancestries (the "width" of this cline is the inverse of the slope at the inflection point; Slatkin 1973; Endler 1977; Fitzpatrick 2013).

Given these predictions, we summarized locus-wise patterns using two clinal parameters: α, which describes the direction of genetic change (i.e. directionally), and β, which indicates the rate of change, or 'width' of a cline. We examined the manner by which these two parameters

varied, then developed hypotheses regarding how those processes impacted our observed population structure. We then considered the evolutionary implications, and limitations, of these results in the context of WTD management.

2 | METHODS

2.1 | Sampling and data collection

During 2016-2019, 1,720 tissues were collected by the Arkansas Game and Fish Commission (AGFC), representing all 75 Arkansas counties. A combination of targeted sampling, road-kill surveys, and a voluntary state-wide CWD testing program were deployed (see Douglas et al., 2020). Age and sex were collected where possible, with the former estimated by tooth development and wear (Severinghaus, 1949). Data for an additional 30 samples were also attained from Wisconsin, as a means to test for signals of historically recorded translocation efforts involving Wisconsin stock (Holder, 1951). From these, a subset of 1,208 samples were chosen for sequencing.

We homogenized tongue or ear tissue (stored at -20°C) and extracted genomic DNA using QIAamp Fast Tissue kits (Qiagen, Inc), with verification via gel electrophoresis (2% agarose). Samples with sufficient yields of high molecular weight DNA (>200ng minimum) were then enzymatically fragmented via incubation at 37°C, using high-fidelity *NsiI* and *MspI* restriction enzymes (New England Biolabs, Inc.), following enzyme and size selection optimization using *in silico* digests (Chafin, Martin, Mussmann, Douglas, & Douglas, 2018) of several available reference genomes hosted by NCBI: *Odocoileus virginianus* (GCA_002102435.1), *Capreolus capreolus* (GCA_000751575.1), and *Capra hircus* (GCF_001704415.1).

Digests were purified using Ampure XP beads (Beckman-Coulter, Inc.) and standardized to 100ng per sample. Unique inline barcodes (Peterson et al., 2012) were then ligated using T4 DNA Ligase (following manufacturer protocols; New England Biolabs, Inc.). Samples were then multiplexed (N=48) prior to automated size selection at 300-450bp using a Pippin Prep (Sage Sciences). Adapter extension was performed over 12 PCR cycles using TruSeq-compatible indexed primers (Illumina, Inc.) and Phusion high-fidelity *taq* polymerase (New England Biolabs, Inc.) Additional quality controls (e.g., qPCR and fragment analysis) were performed on final libraries prior to 1x100 single-end sequencing on the Illumina HiSeq 4000 (Genomics and Cell Characterization Facility, University of Oregon/Eugene), with a total of N=96 samples pooled per lane.

Raw reads were demultiplexed using the pyRAD pipeline (Eaton, 2014), and those with barcode mismatches were discarded. Demultiplexed reads were further filtered by removing those having >4 nucleotides below a quality threshold of 99% accuracy. Reads were then clustered into putative loci within-individuals, allowing for a maximum distance threshold of 15%. This was done using the VSEARCH algorithm (Rognes, Flouri, Nichols, Quince, & Mahé, 2016) as implemented in pyRAD, so as to remove read clusters with 3+ indels, >5 ambiguous consensus nucleotides, or a coverage <20X or >500X. Putative homologs were identified using among-individual clustering with the same parameters, and additionally removing any locus having >2 alleles per individual, >70% heterozygosity for any polymorphic site, >10 heterozygous sites, or <50% individual recovery (see *github.com/tkchafin/scripts* for post-processing and file formatting scripts).

2.2 | Derivation of population structure

We first sub-sampled the dataset to one SNP per locus and excluded those with a minor allele count <2. We then inferred population structure (ADMIXTURE: Alexander et al., 2009) with parallel processing (ADMIXPIPE: Mussmann et al., 2020). Model selection (i.e. for *K*, the number of populations) followed a cross-validation approach with results aggregated from 20 independent replicates (CLUMPAK: Kopelman et al., 2015).

Individual-level ADMIXTURE results were summarized as a 'surface' with spatial discontinuities represented as interpolated assignment probabilities. Here, we constructed state-wide rasters, as representing per-pixel probabilities or 'ancestry proportions,' using Empirical Bayesian Kriging (EBK: ARCMAP 10.7.1, Esri, Inc.). Probability surfaces were then summarized as evenness and diversity of ancestries in a given cell using Simpson's index (Simpson, 1949) (where *K*=number of statewide sub-populations). Our use of the diversity index was based on a straightforward prediction: Areas representing spatial transitions between populations will have a correspondingly low certainty of assignment to a given sub-population ancestry. Likewise, those with low inter-population exchange will be comprised of genetically similar individuals assigned with high probability to the endemic ancestry. Thus, intraspecific suture zones represent a marked transition from one population to another, as identified by site-wise diversity in assignment probabilities (i.e., "ancestry diversity").

We expect spatial variation in ancestry diversity to be inversely proportional to true rates of gene flow, in that this quantity (as well as the ancestry proportions from which it is computed) are a product of gene flow averaged over many generations. Of note is the fact that the method only examines local ancestry probabilities and will not be dominated by translocation-related artefacts (as are methods based on interpolated pairwise genetic distances or F_{ST}). Patterns based on Simpson's diversity were contrasted with those inferred using a form of 2D-stepping stone

model (EEMS; Petkova et al. 2015), which was run with 2 million MCMC iterations (1 million as burn-in), and sampled every 1,000 iterations [following parameter sweeps that tuned MCMC acceptance rates to fall between 20% and 50% (Roberts, Gelman, & Gilks, 1997)].

2.3 | Estimating clinal parameters

We examined the nature of intraspecific suture zones by examining how individual loci transitioned across these regions, relative to the genome-wide average. To do so, we defined eight transects across putative suture zones, sampling 32-73 individuals per transect ($\bar{x}$ =55.38). Individuals were chosen to represent each sub-population using a probability threshold applied to ADMIXTURE results. Loci were filtered to remove all SNPs with missing data in >50% of individuals, and further restricted with regard to computational time by retaining only those loci with a sufficient allele frequency differential [computed as $\delta > 0.50$; (Gregorius & Roberds, 1986)]. Locus-wise clinal patterns were then inferred using a Bayesian method developed originally for hybrid zones (Gompert & Buerkle, 2011, 2012). Open source Python code for filtering SNP matrices and generating necessary input are available at: (*github.com/tkchafin/scripts/phylip2introgress.pl* and *phylip2bgc.pl*).

Analyses were performed for each transect across 4 replicates, each using 1 million MCMC iterations, discarding the first 500,000 as burn-in, with output thinned to every 500 iterations. Results were summarized by visualizing a 2-D density of cline shape parameters. These are: α (=cline center) that describes an increase ($\alpha > 0$) or decrease ($\alpha < 0$) in the probability of locus-specific ancestry from a parental population; and β (=cline rate) that defines the rate of transition in probabilities of locus-specific ancestries having either steep ($\beta > 0$) or wide ($\beta < 0$) shapes (Gompert, Parchman, & Buerkle, 2012). In this context, a locus which does

not deviate from the genome-wide pattern would have α=β=0. Deviation in a directional manner (i.e., an increase or decrease of one ancestry over another) is described by α, whereas deviation in the rate of ancestry change around an inflection point (i.e., sigmoidal) is described by β. Statistical outliers were designated using the method of Gompert and Buerkle (2011). BGC results were parsed and visualized using the ClinePlotR R package (Martin et al. 2020a,b)

2.4 | Relative dispersal by age and sex

Of particular interest in wildlife management is the backwards inference of geographic positioning from genotypes—that is, the geolocation of 'origination' points for sampled animals. This could be used, for example, to ascertain the geographic origin of poached individuals, or to estimate post-natal dispersal. To this end, we used the novel, deep-learning method LOCATOR (Battey, Ralph, & Kern, 2020) to predict the geographic origin of samples without relying upon explicit assumptions about population genetic processes underlying spatial genetic differentiation (Bradburd & Ralph, 2019). This analysis was performed iteratively across each individual, using the remaining samples to train the LOCATOR classifier, with 100 bootstrap pseudo-replicates to assess variance in geolocation. Given computational constraints, we performed the analysis using a subset of 5000 SNPs having a minor allele frequency >10%.

We estimated relative dispersal distances as the Euclidean distance between sampled localities and the centroid of predicted coordinates, under the assumption that the distance between predicted and collection locations is the result of lifetime dispersal, at least for samples for which geolocation variance is low among pseudo-replicates. These results were then partitioned by age, sex and CWD-status.

Our second approach examined the decay in genetic relatedness as a function of distance

from each individual, measured as a Prevosti distance (R-package poppr: Kamvar et al., 2014). Here, the assumption is that recently dispersed individuals will be, on average, more genetically dissimilar from resident individuals, whereas resident individuals having an appreciable reproductive output will be less so. These calculations were limited to individuals that had neighboring samples within a 5km radius, thus implicitly restricting the analysis to high-density sampling regions. We note, however, that the traditional aging method employed for AR WTD (Severinghaus 1949) seemingly has reduced accuracy in older deer, potentially suggesting caution in the interpretation of results (Cook & Hart, 1979; Gee, Holman, Causey, Rossi, & Armstrong, 2002; Mitchell & Smith, 1991).

3 | RESULTS

3.1 | Data processing

Our raw data represented N=1,143 samples, including N=29 from Wisconsin (Table S1). We removed N=83 that had missing metadata, discrepancies with coordinates, or <50% of loci present. Assembly in pyRAD yielded an average of 25,584 loci per sample (σ=8,639). After removing loci present in <50% of samples and excluding those containing potential paralogs (e.g. excessive heterozygosity or >2 alleles per locus), our final dataset contained 35,420 loci, from which 2,655,584 SNPs were catalogued. Of these, 54,102 were excluded as singletons. To limit signal redundancy, we then condensed the data to one SNP per locus, yielded a final matrix of 35,099 SNPs for analyses of population structure.

3.2 | Population structure and ‘ancestry surfaces’

Cross-validation, performed on N=20 replicates each for subpopulation model (*K*=1-20), revealed the optimal number of clusters as *K*=8. Spatial orientation of these samples (Fig. 1) provided a geographic definition, with some subpopulations qualitatively defined by apparent landscape features, such as the Arkansas River Valley as the southern extent of subpopulations *k*=3 and *k*=6.

Two ancestries (*k*1 and *k*8) largely dominated south of the Arkansas River, bounded by Interstate 30 to the north and the Ouachita River to the south (Figs. 1-2), each of which supports the argument that genetic structure is defined by large geographic barriers. The southwestern portion of the state has two ancestral assignments (*k*1 and *k*3), with the latter having mixed representation in the north-central section (potentially an artefact of weak differentiation rather than true shared ancestry). The southeastern section is dominated by a single gene pool (*k*8), which coincidentally subsumed all Wisconsin samples, a strong signature of genetic variability as a residual of historic translocations.

A greater amount of endemic structure occurred in the Ozark Mountains, north of the Arkansas River, where six sub-populations were evident. The most broadly distributed (*k*5) was to the east in the Mississippi alluvial plains, extending westward across the mainstem of the White River then northward towards the confluence of the Black and White rivers, where it grades into several distinct yet loosely defined sub-populations (Figs. 1-2). The northwestern corner of the state was the most heterogeneous, with four primarily endemic gene pools (*k*=2,3,4 and 7; Fig. 2). The northern-most of these was approximately bounded by the White River (Fig. 2), and graded westward into an area of high apparent admixture (Fig. 1). The remaining northwestern region was defined by several gene pools showing considerable admixture and

spatially weak transitions, suggesting reduced gene flow but with geographic and/ or environmental boundaries reasonably porous.

Effective migration surfaces (EEMS) failed to capture any ascertainable pattern relating to spatially defined population structure (Fig. S1). Geographic breaks separating sub-populations (=suture zones) were captured instead by reducing the dimensionality of interpolated assignment probabilities as a continuous Simpson's diversity index (Fig. 3). This, in turn, reflects a dependence on homogeneity of local assignments, rather than global patterns compounded by long-distance transplants.

3.3 | Intraspecific genomic clines

Genomic clines varied substantially among transects (Figs. 4, S2). Most inter-population comparisons within northwest Arkansas, to include *k*2 x *k*3 (both eastern and southern transition zones), *k*2 x *k*6, and *k*4 x *k*7, indicated variation primarily restricted to cline centers (α), with cline steepness (β) at a minimum. The variation in locus-wise pattern for these cases (hereafter termed "α-dominant"), indicated a directional change in the representation of reference populations across the transect, but without a noticeable 'inflection' point, as implied by non-zero cline rates (β).

Remaining comparisons, including one additional transect from northwest Arkansas (*k*3 x *k*4), primarily reflected variation in cline rate (β), in that loci varied most prominently with regard to steepness/width of transition around an inflection point respective to genome-wide ancestry. Although two transects showed minor exception to this pattern (i.e., *k*3 x *k*6 varied along both parameters; and *k*4 x *k*7 showed minimal variation in either), the contrasting variation

between α-dominant versus β-dominant transects suggests that different processes underly ancestry transitions.

3.4 | Estimating dispersal using geolocation analysis

Individuals from densely sampled regions could be assigned to geographic origin using the 'deep-learning' approach, with CWD-positive individuals assigned with a mean bootstrap distance from centroid prediction generally <15km (Fig. S3). However, we did find assignment error (e.g., among bootstraps) was elevated in low-density sampling regions (Figs. 5, S4), which resulted in higher estimated individual dispersal distances (Fig. S4A, B). Given that variance in dispersal estimates dropped considerably below ~25km (Fig. S4C), a conservative threshold of 10km was chosen and all individuals having a mean bootstrap-centroid distance above that were removed for the purposes of dispersal estimates. After filtering, N=110 samples remained (Fig. 5A). A higher error threshold (i.e., 20km) allowed a greater number of total samples to be incorporated (N=264; Fig. 5B), with several collected as 'roadkill' appearing as long-distance transfers. Although these results represent low-precision assignments, they do underscore the capacity of the method with regard to the identification of transported individuals (e.g., as poached or illegally dumped deer, or carcasses transported across state lines or regional management zones).

Geo-located results for those individuals passing a strict error filter demonstrated a dispersal distance for males approximately doubled that of females across all age classes (statistically significant only for the Y2-2.5 class due to low sample sizes; Fig. 6). This pattern was established as early as the Y1-1.5 group, indicating apparent male dispersal by that age.

Smaller dispersal distances were found for fawns across both sexes (Fig. 6), again corroborating *a priori* biological expectations.

Patterns of genetic dissimilarity also showed an age x sex effect, with greater genetic dissimilarity for neighboring Y0-1 males than females, and with a shift towards reduced dissimilarity in males >5 (Fig. S5). This again supports that male deer in Arkansas have dispersed by the Y1-1.5 age class. These results potentially reflect age-biased reproduction as well. Males contributed disproportionately to their local gene pools by age 5 (i.e., producing offspring with resident females), thereby creating a pattern of lower genetic dissimilarity among neighboring individuals, regardless of distance.

4 | DISCUSSION

4.1 | Genetic footprints of historic management

The prolonged history of WTD hunter-harvest, and subsequent long-range translocations into Arkansas and the surrounding region (Ellsworth et al., 1994; Holder, 1951), provide a sideboard to our study in that artificial long-distance movements such as these violate the assumptions inherent with many spatially-explicit methods. However, we found estimates of ancestry diversity and probability surfaces to be qualitatively robust in that they firmly recapitulated the record of historic translocations (Holder, 1951). This, in turn, necessitates an explanation of historic context.

In the early 20th century, following many decades of over-hunting, AR WTD declined to <500 individuals (Holder, 1951). In response, Arkansas Game and Fish Commission (AGFC) implemented an extensive restocking program (1941-1951) by establishing three primary sources as its basis. The first was Howard County WTD farm (southwestern Arkansas; Fig. 7),

established from locally transplanted central Arkansas individuals (Wynn, 1943). It is now located within the epicenter of population *k*1 (Figs. 2, 7), with ancestry shared elsewhere in the state, thus supporting it as a local translocation epicenter.

A second major source was the Sylamore District (Ozark Mountains; Wood, 1944; Holder, 1951), where individuals were naturally abundant (Fig. S7). Individuals from this region have a consistently higher probability of assignment to *k*3 (Figs. 2, 7), where records indicate ~81% of repopulated individuals in the Gulf Coastal Plain originated from the Sylamore cluster (Holder, 1951; Karlin, Heidt, & Sugg, 1989; Wood, 1944). Our analyses are in agreement, in that many individuals in southwestern Arkansas (Figs. 1, 6) reflect a mixed assignment to the "Sylamore" cluster. They also comprised ~36% of stocking efforts in the Mississippi Delta region (Karlin et al., 1989).

Our results also indicate some mixed assignment of individuals to *k*3, although a more widespread representation is found in *k*5. AGFC surveys (~1942-1945) indicate WTD as relatively abundant in the southeastern Delta region (Figs. 7, S7), allegedly linked with re-population efforts following the disastrous 1927 Mississippi flood. This event, coupled with over-hunting, nearly extirpated WTD in the region, save small numbers sustained by local sportsmen (Holder, 1951; Fig. S7). We hypothesize WTD in the Delta region largely descended from those efforts, given the contemporary homogeneity of ancestry assignment for this region.

A third (extraneous) WTD source was the Sandhill Game Farm (Babcock, WI; Wood 1944). Records indicate that ~64% of releases into the Mississippi Delta region originated out-of-state, the majority from Wisconsin (Holder, 1951; Karlin et al., 1989). Our Wisconsin samples were unanimously assigned to a gene pool prominently represented in the southern Delta region (*k*8; Fig. 2), firmly establishing its genetic legacy as extending from imported deer.

Mitochondrial haplotypes putatively originating from Wisconsin were also uncovered in Missouri, Kentucky, and Mississippi (Budd, Berkman, Anderson, Koppelman, & Eggert, 2018; DeYoung et al., 2003; Doerner et al., 2005).

All genetic 'clusters' that lacked spatial cohesion in our analyses can be connected to the three major stocking sources involved in earlier restoration efforts (per reference to historic records). The remaining sub-populations, primarily in the Ozarks (*k*2, 4, 6, and 7) may represent natural re-colonization from refugial populations (Figs. 2, 7), an hypothesis supported by early census data (Figs. S7, S8).

4.2 | Landscape-drivers of contemporary population structure

A primary focus in our study was the contemporary genetic structure of AR WTD, especially with regard to the manner by which these data promote landscape resistance and potentially constrain CWD infection (Hemming-Schroeder, Lo, Salazar, Puente, & Yan, 2018; Kelly et al., 2014). Yet several prerequisites are apparent in this regard. For example, one question which is apparent but previously constrained by technological limitations is the degree to which potential patterns of genetic variability in WTD have been conflated by anthropogenically-mediated translocations.

We addressed this issue by utilizing next-generation molecular techniques to derive highly variable SNP markers. We also implemented advanced geospatial procedures that visualized the spatial transitions inherent within WTD ancestry in such a way that translocation histories were not a limiting factor. We did so by interpolating our assignment probabilities from ADMIXTURE, then applying Simpson's diversity index as a means of reducing the dimensionality of these probabilities. We also examined locus-specific patterns within our

434 transitions so as to polarize stochastic versus deterministic processes.

Previous studies concluded that landscape genetic inferences were limited at best, due to
436 complex interactions between historic translocations and subsequent population growth (Leberg et al. 1994; Leberg and Ellsworth 1999; Budd et al. 2018). However, many of these studies relied
438 upon (now) obsolescent molecular markers (e.g., mtDNA or reduced panels of microsatellite DNA markers) that captured substantially less polymorphism than do next-generation methods
440 (Hodel et al., 2017; Jeffries et al., 2016; Lemopoulos et al., 2019). Subsequent studies at finer spatial scales have supported the role of large-scale geomorphic configurations (e.g., rivers,
442 highways) as semipermeable barriers to WTD gene flow (Kelly et al., 2014; Locher et al., 2015; Miller et al., 2020; Robinson et al., 2012), despite the potential complication caused by re-
444 stocking efforts, and in accordance with radio-telemetry data (Peterson et al., 2017).

Spatio-genetic patterns can still be informative with regards to landscape-level dispersal,
446 despite rapid transitions between historical and contemporary conditions (Epps & Keyghobadi, 2015) which might be expected to obfuscate relationships. For example, spatial genetic patterns
448 in invasive species are also attributable to large-scale environmental features, despite oft-reduced levels of genetic diversity (Lopez, Hurwood, Dryden, & Fuller, 2014; Sacks, Brazeal, & Lewis,
450 2016; Zalewski, Piertney, Zalewska, & Lambin, 2009). The same can be said for populations occupying landscapes defined by recent anthropogenic developments, such as large urban
452 centers, suggesting the potential for such patterns to rapidly emerge (Beninde et al., 2016; Combs, Puckett, Richardson, Mims, & Munshi-South, 2018; Kimmig et al., 2020). In the case of
454 translocation, the magnitude of analytical artefacts are expected to be both scale-dependent, and a function of the specific analytical assumptions. For example, classic tests of ‘isolation-by-
456 distance’ implicitly assume a negative relationship between geographic proximity and pairwise

patterns of genetic distance (Meirmans, 2012; Rousset, 1997). Here, translocations are demonstrably inconsistent with this expectation.

The assignment method used in our study yielded patterns of genetic similarity that reflected translocations as depicted in historic records (Fig. 7). We sought to effectively 'remove' this artificial signal so as to more appropriately expose landscape features that could potentially modulate deer dispersal. Our approach (i.e., reducing dimensionality of assignment probabilities) produces relatively straightforward predictions about the ensuing metric: Areas with an elevated flux of individuals should have elevated homogeneity with regard to interpolated ancestry assignment (i.e., ADMIXTURE ancestry proportions). By the same logic, regions that reflect transitions in ancestry proportions would also demonstrate reduced homogeneity. Although spatial assignments can also be vulnerable to artefacts, such as the over-fitting of discrete clusters within otherwise continuous populations (Bradburd et al., 2017), they effectively identify linear barriers to gene flow (Blair et al., 2012). Coincidentally, our approach to dimensionality-reduction also revealed numerous linear subdivisions that aligned with major landscape barriers, such as Arkansas rivers (Fig. 3). Other putative transitions approximately corresponded with large urban centers.

4.3 | Separating stochastic versus deterministic processes in clinal patterns

It is difficult to disentangle contemporary demographic processes (versus analytical idiosyncrasies) in the formation of these patterns. As a means of clarification, we generated multi-locus genomic patterns (Epps & Keyghobadi, 2015) under the expectation that observed deviations of locus-wise clines from the genome-wide average would dictate the relative importance of stochastic versus deterministic processes (Barton, 1983; Barton & Hewitt, 1985;

480 Slatkin, 1973; Vasemägi, 2006). We found eight transects that varied in either the width of locus-wise transitions (β), or the direction of change in allele representation (α). Interestingly, 'α-
482 dominant' transects were found within the Ozark region, previously hypothesized as being naturally re-colonized from local refugia (i.e., *k*2 x *k*3E/S, *k*2 x *k*6, and *k*4 x *k*7; Figs. 4, S2). This
484 hypothesis is also supported by state-wide surveys (1940's) that found occupied WTD habitat roughly corresponding with each Ozark sub-population (Figs. 7, S8).

486 All transects displayed near-zero β values across loci as well, suggesting either stochastic processes (genetic drift, bottlenecks) or sampling artefacts as drivers of ancestry transitions,
488 given our expectation that a 'true' hard barrier between discrete populations would yield an under-representation of inter-population heterozygotes (as described by β).

490 One interpretation of this result is that genetic drift at the edge of an expanding refugium creates a 'rolling' founder effect, with alleles being over-represented ($\alpha>0$) or under-represented
492 ($\alpha<0$) across the re-colonized territory (Excoffier & Ray, 2008; Hallatschek & Nelson, 2008). This phenomenon—termed "gene surfing"—can generate wholly neutral patterns that appear to
494 be adaptive (Peischl, Dupanloup, Bosshard, & Excoffier, 2016; Travis et al., 2007), and may explain the presence of numerous α-outlier loci in those transects (Fig. 4).

496 Interestingly, all of our β-dominant transects crossed major rivers: Transect *k*3 x *k*6 spanned the Arkansas River; *k*3 x *k*5 the White River; and *k*1 x *k*8 the Ouachita River. Transect
498 *k*3 x *k*4 crosses the smaller Buffalo River, which may explain the depressed variability in cline steepness (Fig. 4). Non-zero β values implicate variations on a sigmoidal cline shape, with values
500 describing rates of change in allele frequencies that are either steep ($\beta>0$) or wide ($\beta<0$).

Classically, clinal patterns are established by selection, or the existence of hard
502 boundaries to gene flow (Endler, 1973; Slatkin, 1973). However, spatially variable gene flow

coupled with drift can generate clinal patterns without necessitating selection across a considerable proportion of the genome (Vasemägi, 2006). Selection could feasibly be involved, at least for regions involving translocation of WTD subspecies, in that crosses between subspecies have elicited fitness impacts such as dystocia (abnomal maternal labor due to shape, size, or position of the fetus; Galindo-Leal and Weber 1994). Previous studies have also underscored the genetic cost of inter-subspecific stocking (Hopken, Lum, Meyers, & Piaggio, 2015), such as anomalous variability in breeding time among other southern-recovered WTD populations (Sumners et al., 2015). Some limited evidence also exists for a pheromonal basis for reproductive isolation among mule deer subspecies [*Odocoileus hemionus*; (Müller-Schwarze & Müller-Schwarze, 1975)].

4.3 | Hunter-harvest and its management implications

Our results identify within AR WTD a diagnosable genetic signature of historic translocations within the genomes of extant populations. This simultaneously underscores the success of early restocking efforts, while also reiterating long-standing concerns about the genetic and/ or phenotypic impacts of anthropogenic translocations (Meffe & Vrijenhoek, 1988). It also reinforces the need to formalize as an explicit management consideration the intraspecific taxonomy of WTD, both to better understand the (yet to be seen) evolutionary consequences of past translocations, and to provide a more proactive baseline going forward (Cronin, 2003; Gippoliti, Cotterill, Groves, & Zinner, 2018).

Resource agencies, in particular, should prioritize those populations that retain endemic genetic diversity, and by so doing, tacitly acknowledge the importance of preserving this evolutionary legacy. Such recognition would capitalize on the many years of natural selection

that have operated on those populations prior to anthropogenic interference. It would also open the door for potential variation in hunter-harvest, such as by having a restricted season strictly for 'legacy' AR deer.

Our patterns of age- and sex-biased dispersal distances (Fig. 5, 6) largely recapitulate expectations based on WTD life-history: Male dispersal established by the yearling cohort (Long et al., 2008; McCoy, Hewitt, & Bryant, 2005; Shaw, Lancia, Conner, & Rosenberry, 2006); females lack age-dependent dispersal (Lutz et al., 2015). The potential utility of the approach lies within the context of a multi-state genetic monitoring program for WTD. While this would necessitate inter-state investment and coordination, potential benefits of a 'next-generation' approach would be in preserving the evolutionary heritage of WTD, supporting the adaptive management of a biodiversity resource of national importance, as well as promoting the strong tradition of hunting in North America (Geist, Mahoney, & Organ, 2000).

4.4 | CWD expansion and its management implications

Our results also suggest the existence of several discontinuities in gene flow across the state. Given that CWD is a paramount issue in the global management of WTD (Rivera, Brandt, Novakofski, & Mateus-Pinilla, 2019; Uehlinger, Johnston, Bollinger, & Waldner, 2016), a valuable application of our results would be towards disease containment. Given that the spread of CWD will be more rapid within rather than among populations, monitoring efforts should focus on detecting 'breaches' between genetically distinct regions (which are most often divided by major rivers and urban centers, as herein; Fig. 3). Interestingly, the current boundaries for the AGFC 'Deer Management Units' (DMUs) (Meeker et al., 2019), are remarkably consistent with many of the intraspecific suture zones identified in our study. Thus, potential mitigation efforts

should work to constrain the transportation of potentially infectious material (such as carcasses) from CWD-detected DMUs. Management actions should reduce the outward dispersal of individuals from DMUs, and one approach is to reduce the density of yearling males, which often comprise >50% of emigrating individuals (McCoy et al., 2005; Nelson, 1993; Nixon, Hansen, Brewer, & Chelsvig, 1991). A similar action could be management to reduce local population densities. The latter, in turn, acts to drive dispersal in that robust population numbers are a catalyst for increasing social pressure as well as resource competition (Long et al., 2008; Lutz et al., 2015; Shaw et al., 2006).

One harvest strategy [‘Quality Deer Management,’ QDM; (Brothers and Ray, 1975; Hamilton et al., 1995)] has several management goals operating in parallel to improve WTD demography. These are: Actively decreasing overall population density; elevating the proportion of mature males in the population; and increasing the female component of the sex ratio. The success of this approach was assayed by evaluating WTD emigration rates pre- and post-application (Shaw et al., 2006). Two important aspects were noted: Emigration probabilities decreased, as did mating behavior of yearling males. The implications of a management strategy focusing on these explicit goals would be a serious reduction in CWD dissemination. It is unclear how this paradigm could impact long-term disease trajectories within CWD-prevalent DMUs, although lower emigration probabilities and decreased densities would concomitantly depress the probability of disease contraction for a given individual.

4.5 | Selection for CWD genetic variants and its management implications

Previous CWD research in WTD populations has focused on the prevalence of a polymorphism in the *PRNP* gene [responsible for the malformed protein product that constitutes the prion agent

of CWD (Johnson et al., 2011; Race, Meade-White, Miller, Fox, & Chesebro, 2011; Rivera et al., 2019)]. Those WTD exhibiting a non-synonymous transition at amino acid residue 96 (from G to S) had decreased susceptibility to CWD. This variant had a significantly greater presence among older individuals in CWD-detected areas, suggesting increased survivability for those individuals manifesting that variant (Chafin et al., 2020; Douglas et al., 2020). Results herein support this result, in that older males (>4 years) are genetically more similar to neighboring individuals than to younger males (Fig. S6). This in turn suggests a non-linear increase in reproductive success with age [or perhaps with other collinear factors as well, such as body weight or antler size (Newbolt et al., 2017)].

Directing management efforts towards an older age-structure could therefore have an ancillary benefit in that it would promote the relative reproduction of individuals having the 96S variant, given its presence at a significantly higher probability among more mature individuals (Douglas et al. 2020b). Our results could also be used to explore those environmental variables potentially responsible for resistance to movement at the landscape-level. This aspect, in conjunction with ongoing work on spatially variable genetic susceptibility, could promote the development of risk assessment models that assay disease spread.

DATA AVAILABILITY STATEMENT

All raw sequence files will be accessioned in the NCBI Sequence Read Archive (SRA) under BioProject XXXXXX following acceptance; relevant curated (i.e. assembled and filtered) data will be archived on Dryad (doi: XXXXXX); codes and custom scripts developed in support of this work are also available as open-source via GitHub under the GNU Public License: github.com/tkchafin (and as cited in-text).

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Figures and Tables

Figure 1: **Ancestry proportions for 1,143 Arkansas white-tailed deer**, as inferred using the program ADMIXTURE. Samples are represented as pie charts plotted at absolute collection coordinates, with colors of assignment probabilities proportional to a particular subpopulation.

Figure 2: **Assignment probabilities for eight populations (*k*=1 through *k*=8)**, interpolated using Empirical Bayesian Kriging. P(*k*)=1.0 corresponds to 100% probability of ancestry per raster cell, and P(*k*)=0.0 corresponds to 0%. Individual samples are represented as black dots.

936 **Figure 3: Simpson's diversity of interpolated ancestry proportions.** Each raster cell was assigned 8 values equal to the expected proportion of ancestry corresponding to the 8 genetic
938 clusters (Fig. 1), then summarized by calculating Simpson's diversity index.

940 **Figure 4: Relationships between genomic cline parameters** contrasted among eight sub-sampled transects =of intraspecific suture zones in white-tailed deer (Fig. 3). Contour plots show
942 relative densities of SNPs varying in cline rate (β), representing the steepness of clines, and cline center (α), representing bias in SNP ancestry. Outlier loci are highlighted in blue.

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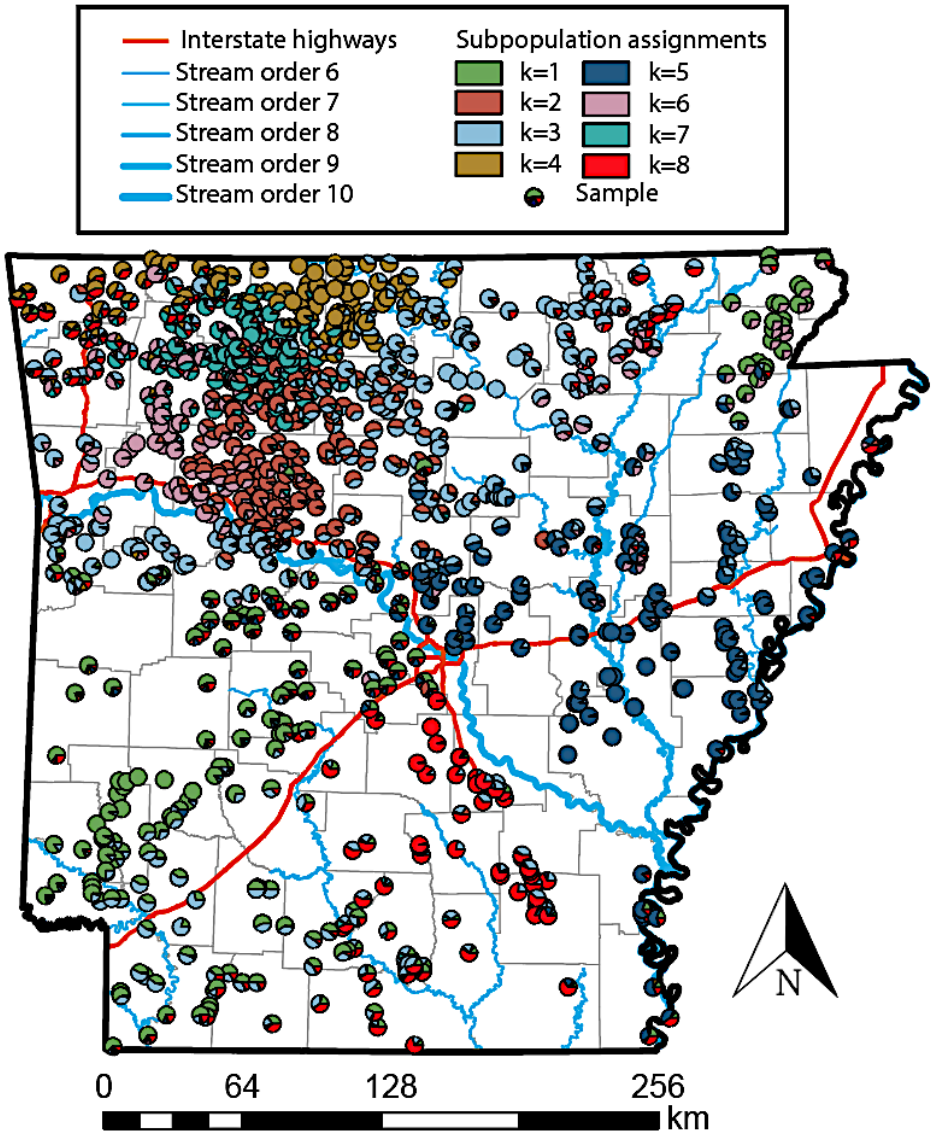
Figure 5: Summary of geo-location predictions in LOCATOR as a random subset of N=490
946 individuals, at two error thresholds: 10km (=A) and 20km (=B), thus constraining results to N=110 (=A) and N=264 (=B). Error calculated as mean distance of bootstrap predictions from
948 the centroid predicted for each individual (see Fig. S4). A black dot denotes the predicted location of an individual and a colored dot indicates the 'true' location (colors proportional to
950 measurement error in km).

952 **Figure 6: Inferred dispersal distances, partitioned by sex and age class**. Dispersal distances were calculated as the difference (in km) between the predicted and true locations, excluding all
954 individuals with a mean prediction error of 10km (see Figs. 14-15). Sample sizes for each group are given in black, with the mean in red below each box plot. P-values are reported for within-
956 age two-sample t-tests comparing means from males and females.

958 **Figure 7: Proposed translocation pathways and refugial populations in Arkansas**, showing (left) translocation events supported by genetics along (dashed line), as well as those with
960 anecdotal support given limited historical records (solid), from three primary stocking sources: Sandhill Game Farm in Wisconsin (W); 'Sylamore District' state refuge sites (S); and the
962 Howard County Game Farm (H). Also shown are major inhabited regions of white-tailed deer (right) estimated from 1942-47 game surveys, excluding small regions (see full version in Online
964 Supplementary Material). Putative inhabited regions are also annotated according to their hypothesized associations with contemporary genetic clusters (Fig. 1-2).



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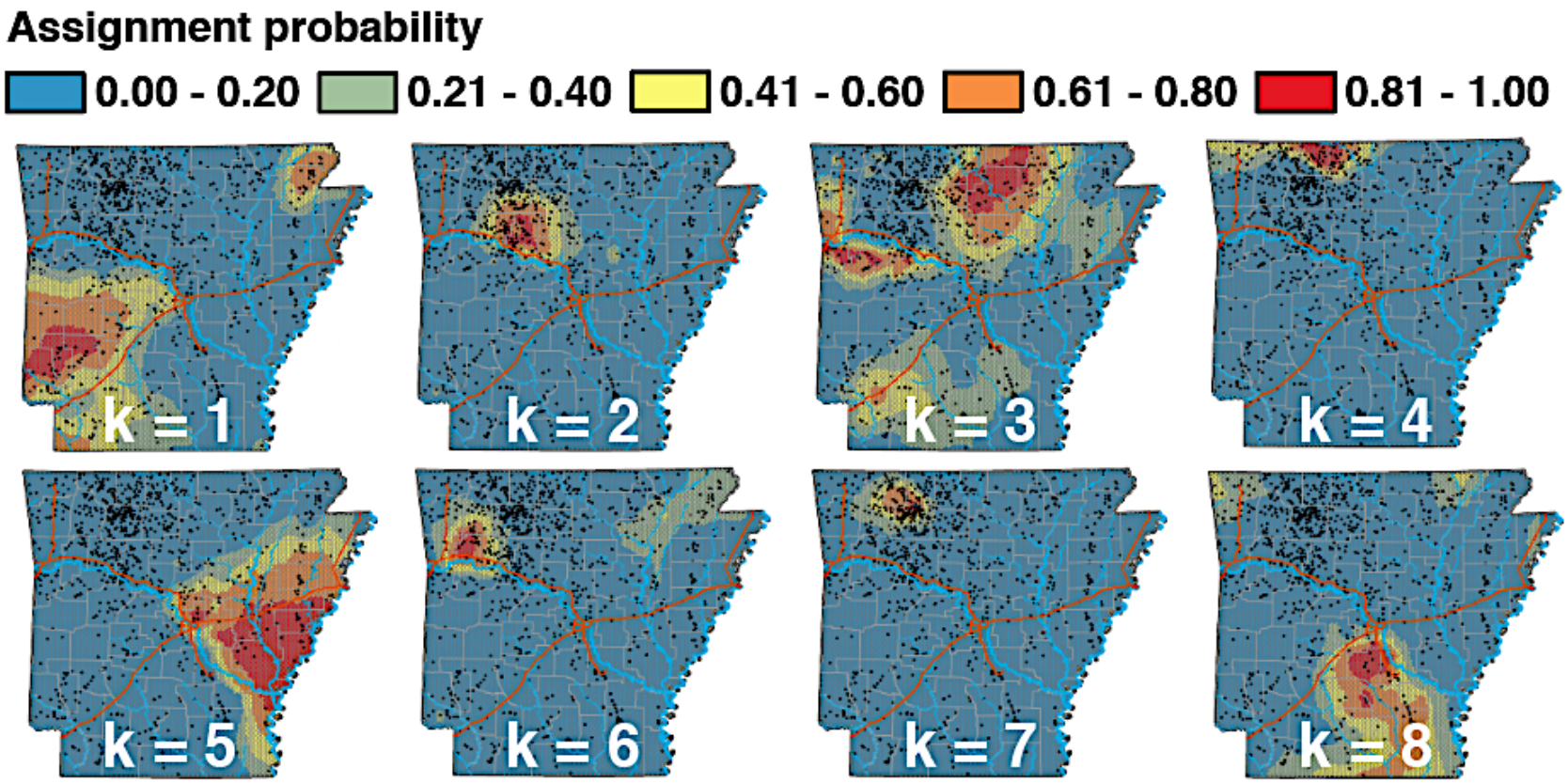

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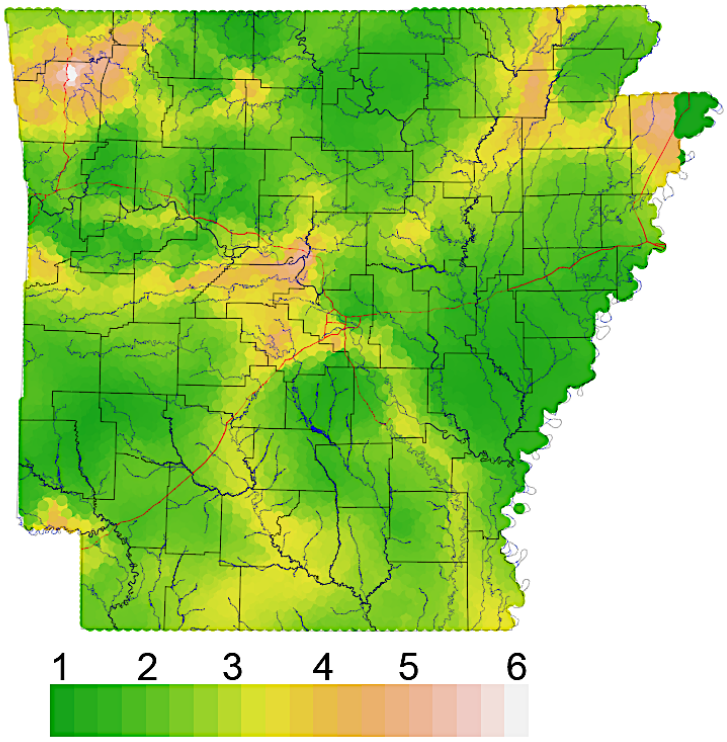

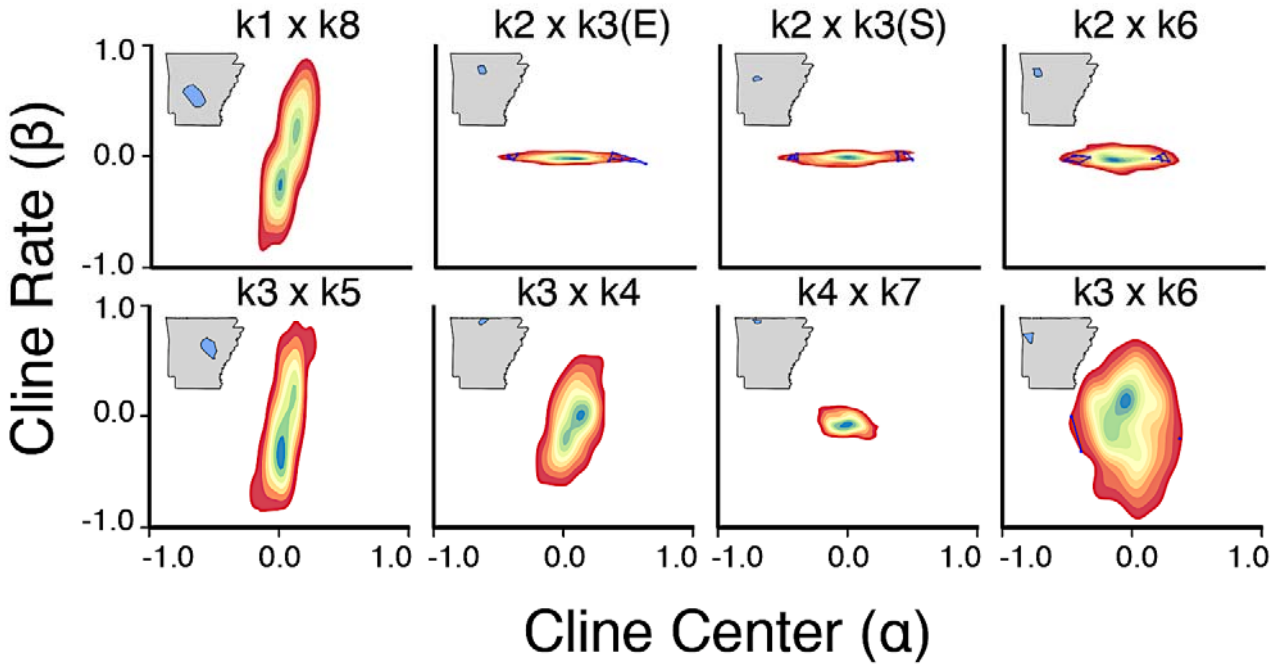

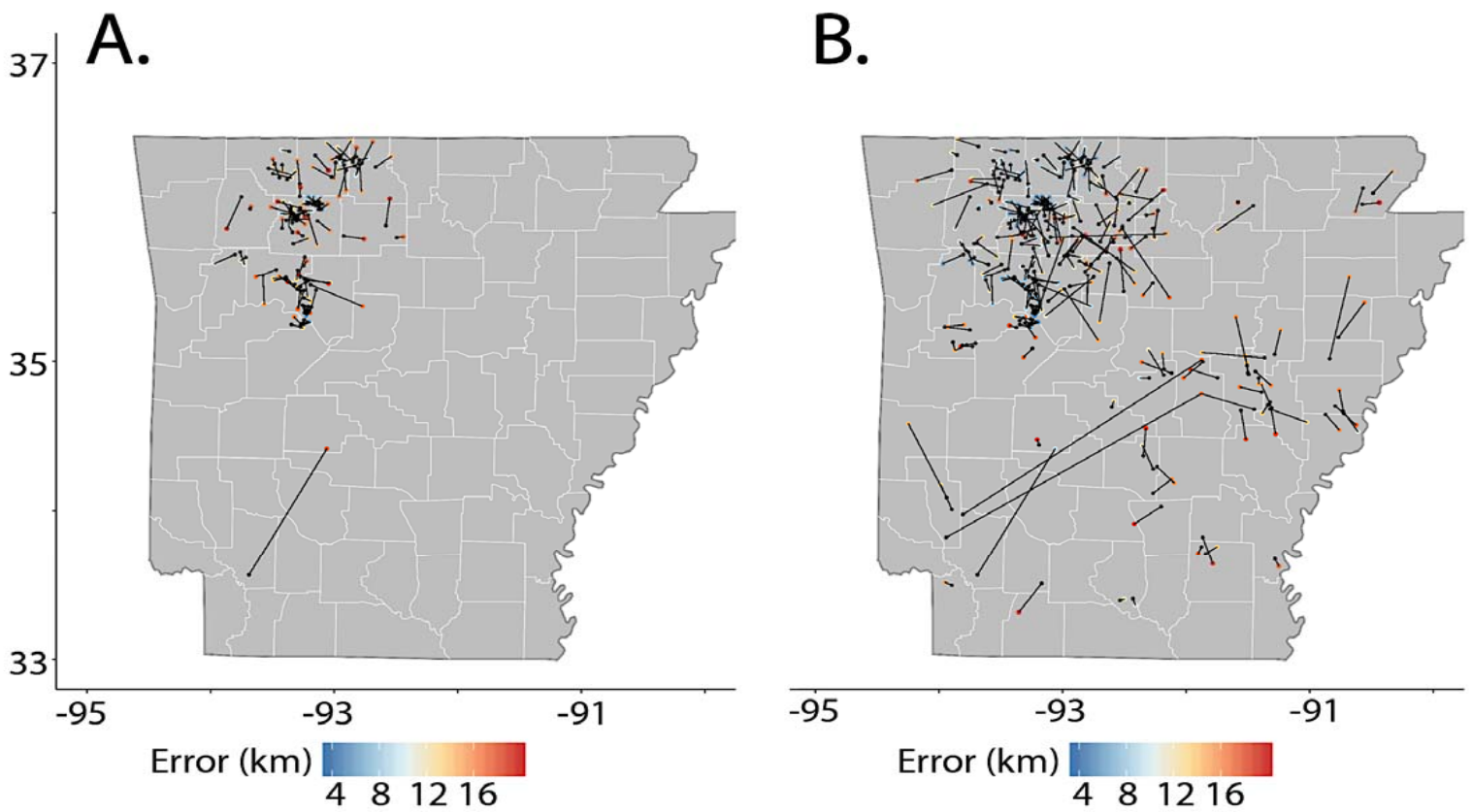

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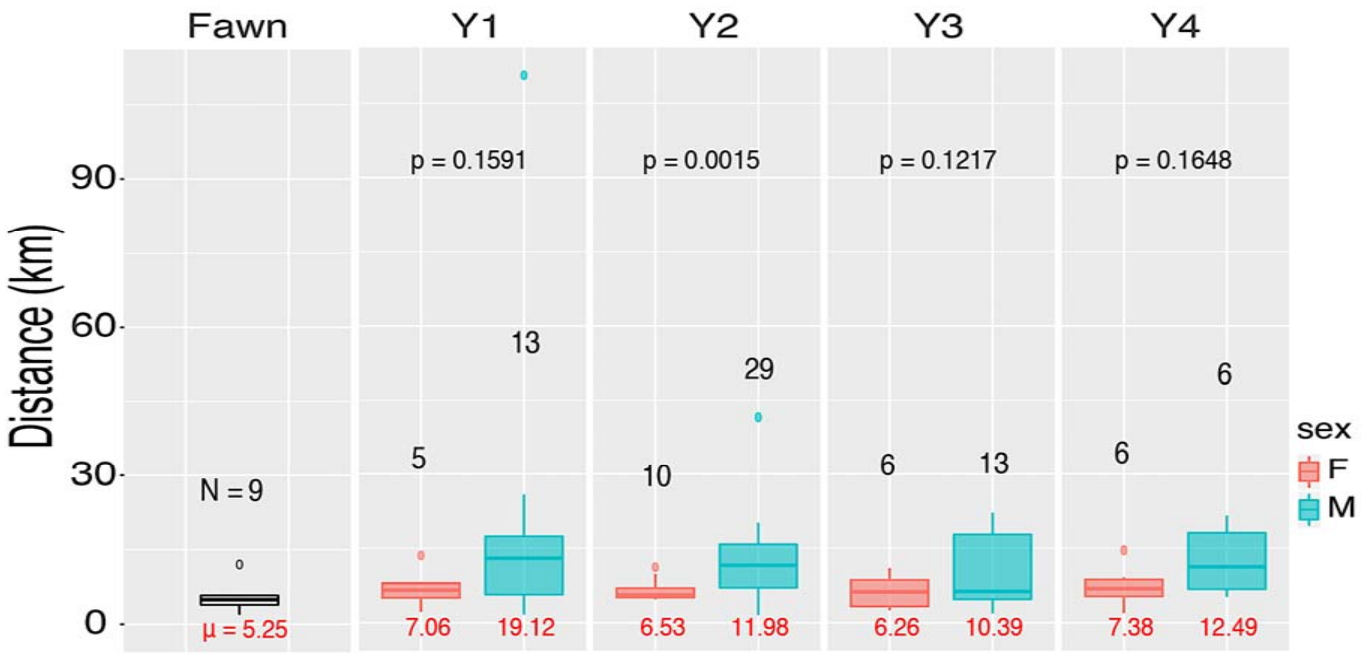

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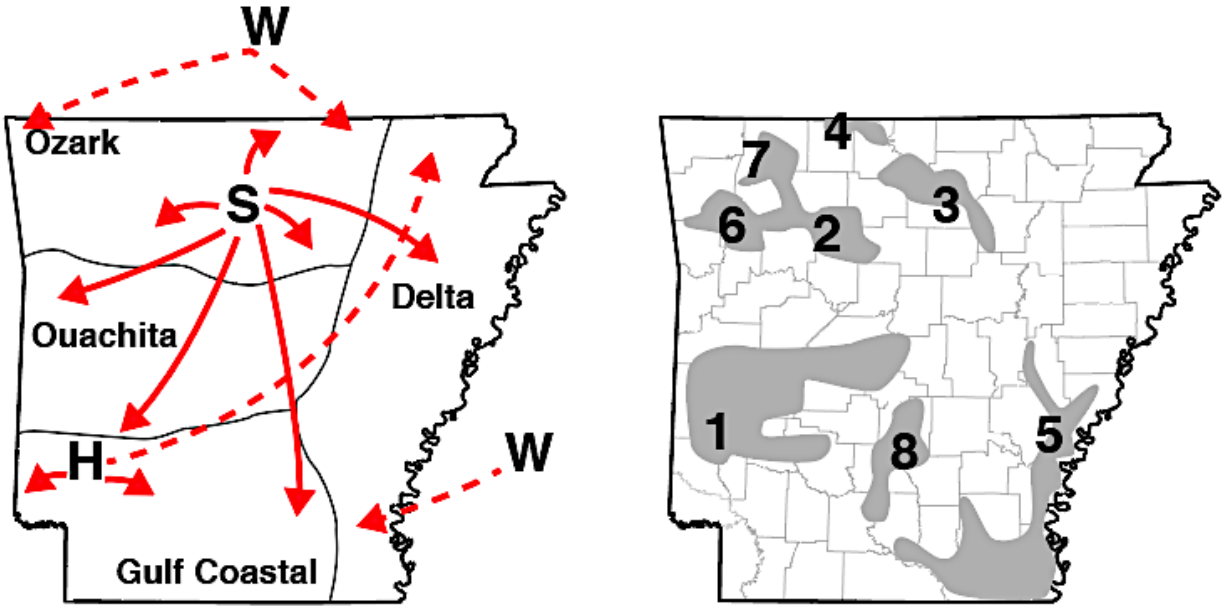

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Supplementary Figures and Tables

Table S1: Numbers (=N) of white-tailed deer genotyped across ~35,000 SNP loci. Samples were collected from 75 counties (=County) in Arkansas (2016-2019). Code indicates standard 2-letter county abbreviation. Samples removed due to missing data are not included.

County	Code	N	County	Code	N
Arkansas	AR	11	Lee	LE	9
Ashley	AS	1	Lincoln	LI	8
Baxter	BA	19	Little River	LR	10
Benton	BE	19	Logan	LO	32
Boone	BO	34	Lonoke	LN	11
Bradley	BR	2	Madison	MA	39
Calhoun	CA	14	Marion	MR	39
Carroll	CR	50	Miller	MI	8
Chicot	CH	3	Mississippi	MS	2
Clark	CL	7	Monroe	MO	10
Clay	CY	15	Montgomery	MN	2
Cleburne	CE	8	Nevada	NE	13
Cleveland	CV	5	Newton	NW	140
Columbia	CO	4	Ouachita	OU	12
Conway	CN	11	Perry	PE	8
Craighead	CG	7	Phillips	PH	9
Crawford	CW	6	Pike	PI	8
Crittenden	CT	8	Poinsett	PO	10
Cross	CS	10	Polk	PL	3
Dallas	DA	7	Pope	PP	62
Desha	DE	11	Prairie	PR	10
Drew	DR	14	Pulaski	PU	11
Faulkner	FA	14	Randolph	RA	8
Franklin	FR	20	Saline	SA	11
Fulton	FU	9	Scott	SC	2
Garland	GA	14	Searcy	SE	32
Grant	GR	5	Sebastian	SB	17
Greene	GE	16	Sevier	SV	12
Hempstead	HE	9	Sharp	SH	16
Hot Spring	HS	3	St. Francis	SF	7
Howard	HO	11	Stone	ST	15
Independence	IN	7	Union	UN	6
Izard	IZ	6	Van Buren	VB	23
Jackson	JA	2	Washington	WA	17
Jefferson	JE	13	White	WH	10
Johnson	JO	45	Woodruff	WO	9
Lafayette	LA	14	Yell	YE	31
Lawrence	LW	17	**Total**		**1,143**

Figure S1: **Effective migration rates and intra-population diversity** (log_{10} scale), calculated from effective migration surfaces (EEMS). Rates are plotted according to colored bin, with divisions calculated as natural breaks using the Jenks algorithm in ArcMAP.

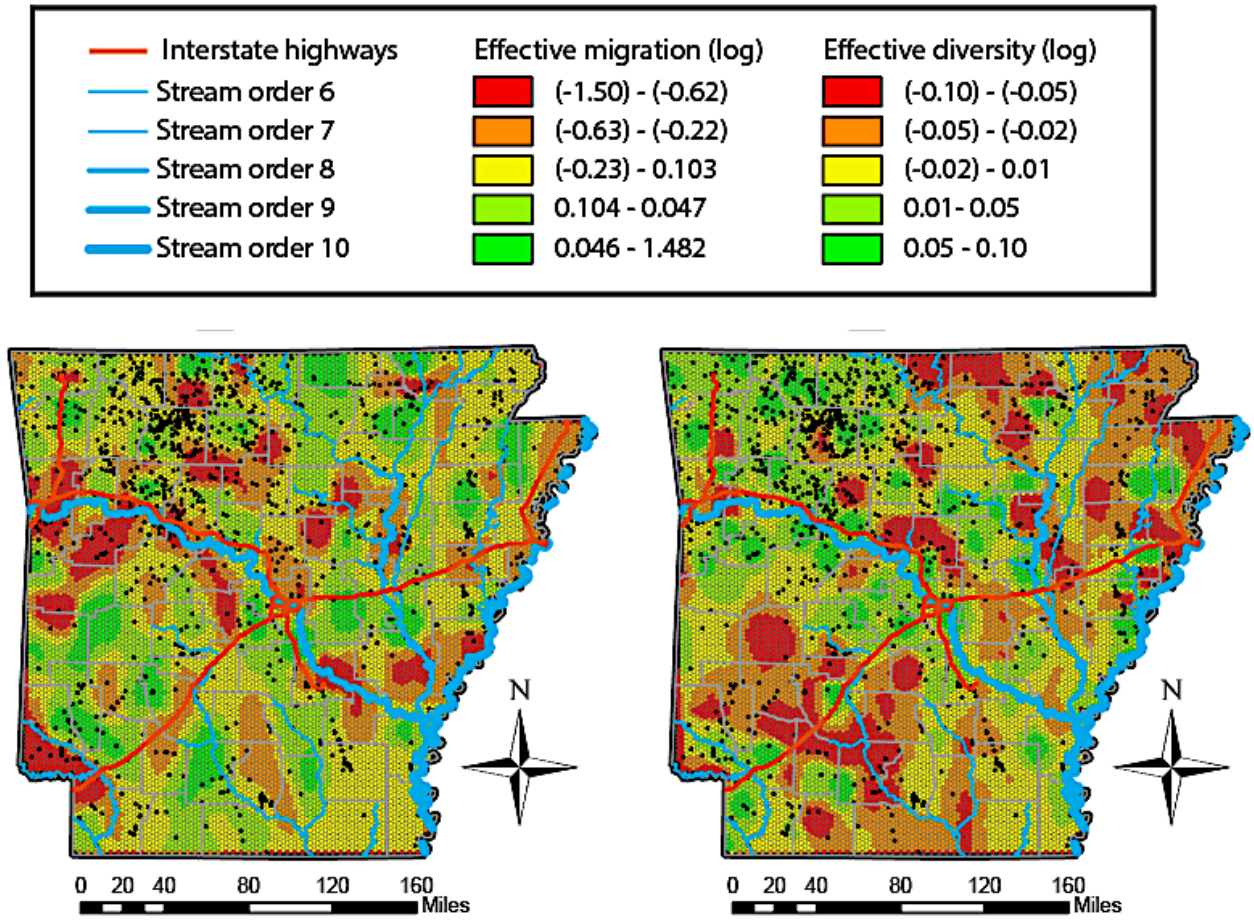


Figure S2: Sampled transects employed for genomic cline analysis with selected groups within each coalesced within colored hulls: Reference population 1 (p1; red); Reference population 2 (p2; green); and putative admixed individuals (popA; blue).

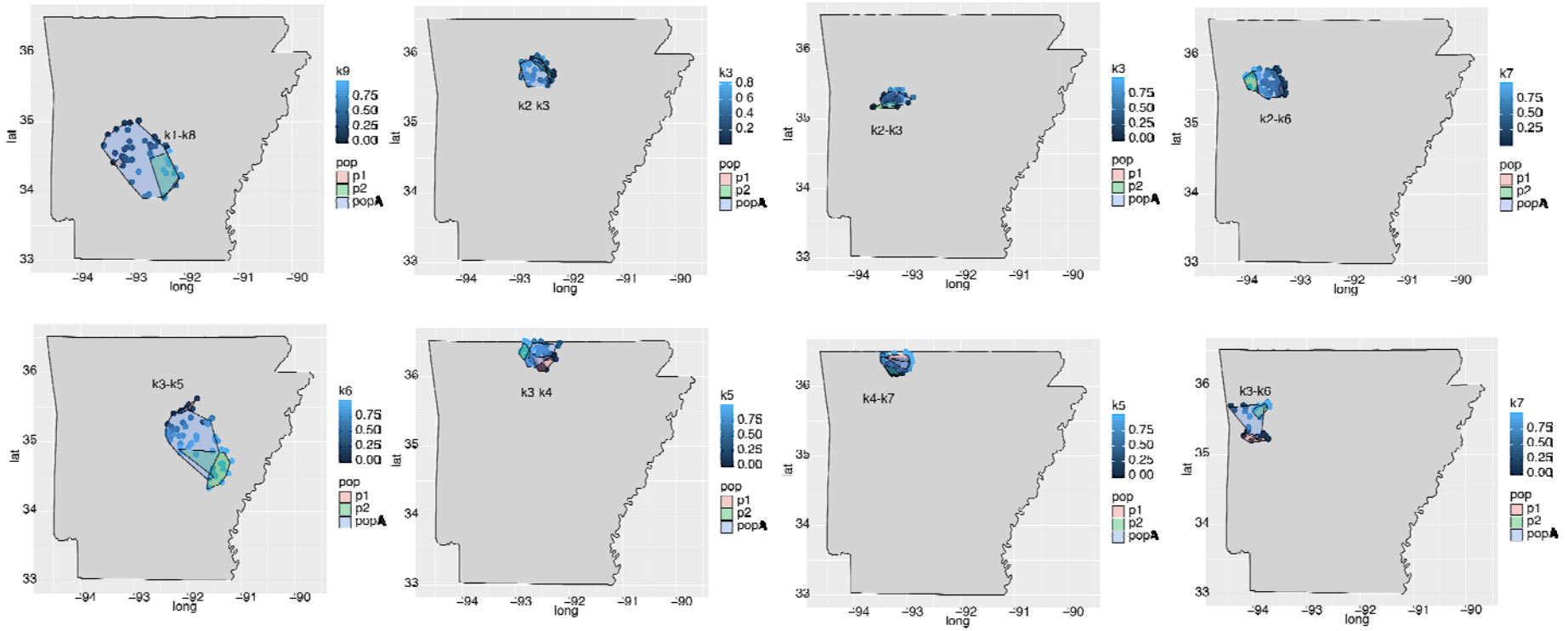


Figure S3: LOCATOR Geo-located results for CWD-positive individuals derived via LOCATOR. Individuals are represented by dots, pairs of which are connected by a single line. A black dot denotes predicted location, while a colored dot indicates 'true' (observed = sampled) location (color proportional to distances separating each). Inserted figures offer full prediction results for three selected samples, with bootstrap estimates demarked by a 95% contour.

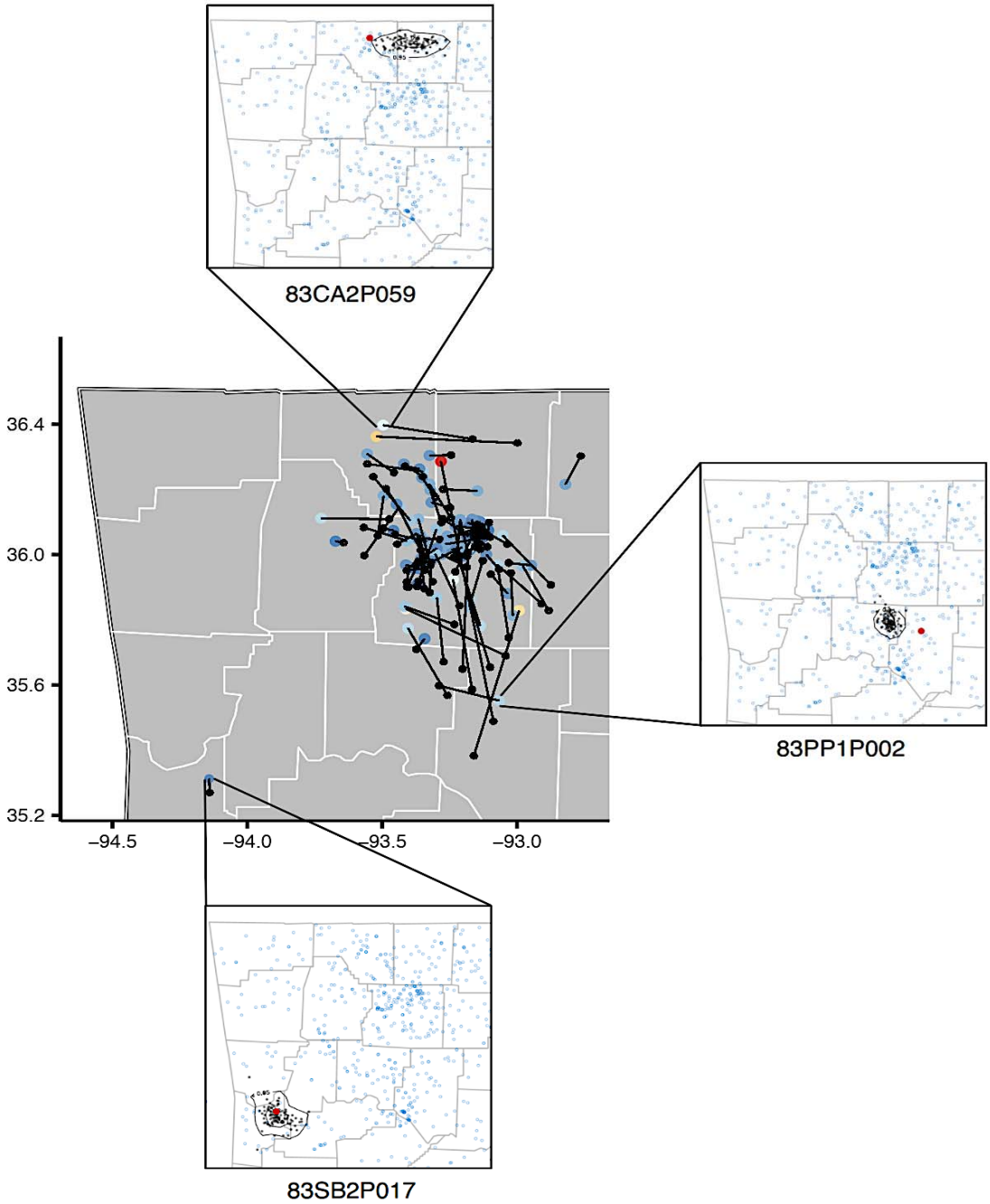
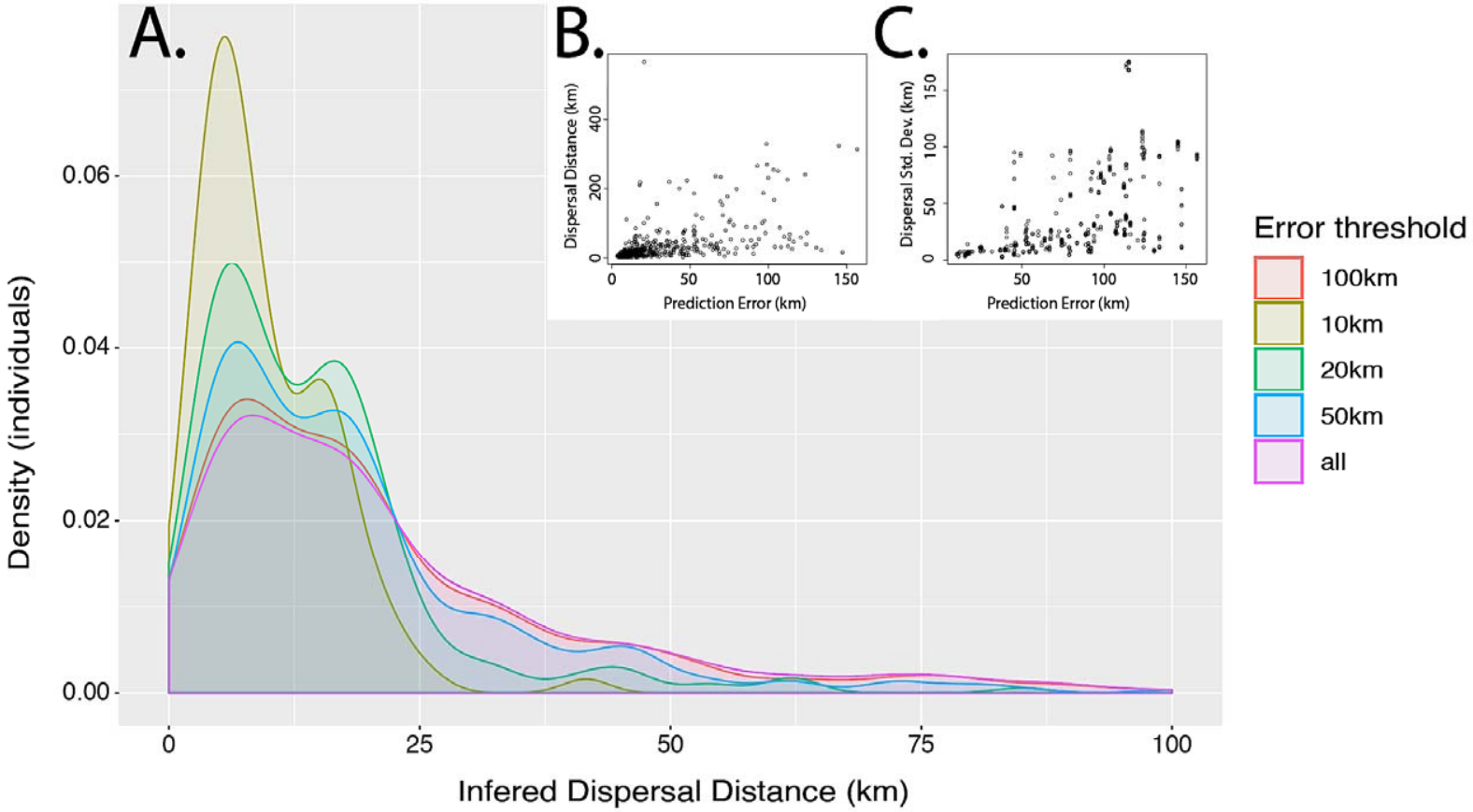


Figure S4: Effects of error thresholds on inferred dispersal distances as predicted by LOCATOR analysis. Inferred dispersal kernels were computed at several error thresholds: (A) Error computed as mean distance of predicted coordinates for each individual at 100 bootstrap estimates from predicted centroid (=interpretation of localized vs. dispersed predictions). Dispersal distances calculated as difference (in km) between predicted centroid versus 'true' (observed) location. Inferred dispersal distances generally increase for individuals with larger prediction error; (B) Larger stochastic variation in centroid location for individuals with lower predicted precision among bootstraps; (C) Standard deviation of dispersal distances for the latter computed in a sliding window of 10km along the x-axis (prediction error).



1010 **Figure S5: Spatial patterns of genetic dissimilarity among white-tailed deer partitioned by age and sex.** Genetic distances between individuals and neighbors derived from 5,000 randomly
1012 sampled SNPs depicted across physical distance (x-axis). Results depict different cohorts of males (A) and females (B) by age.
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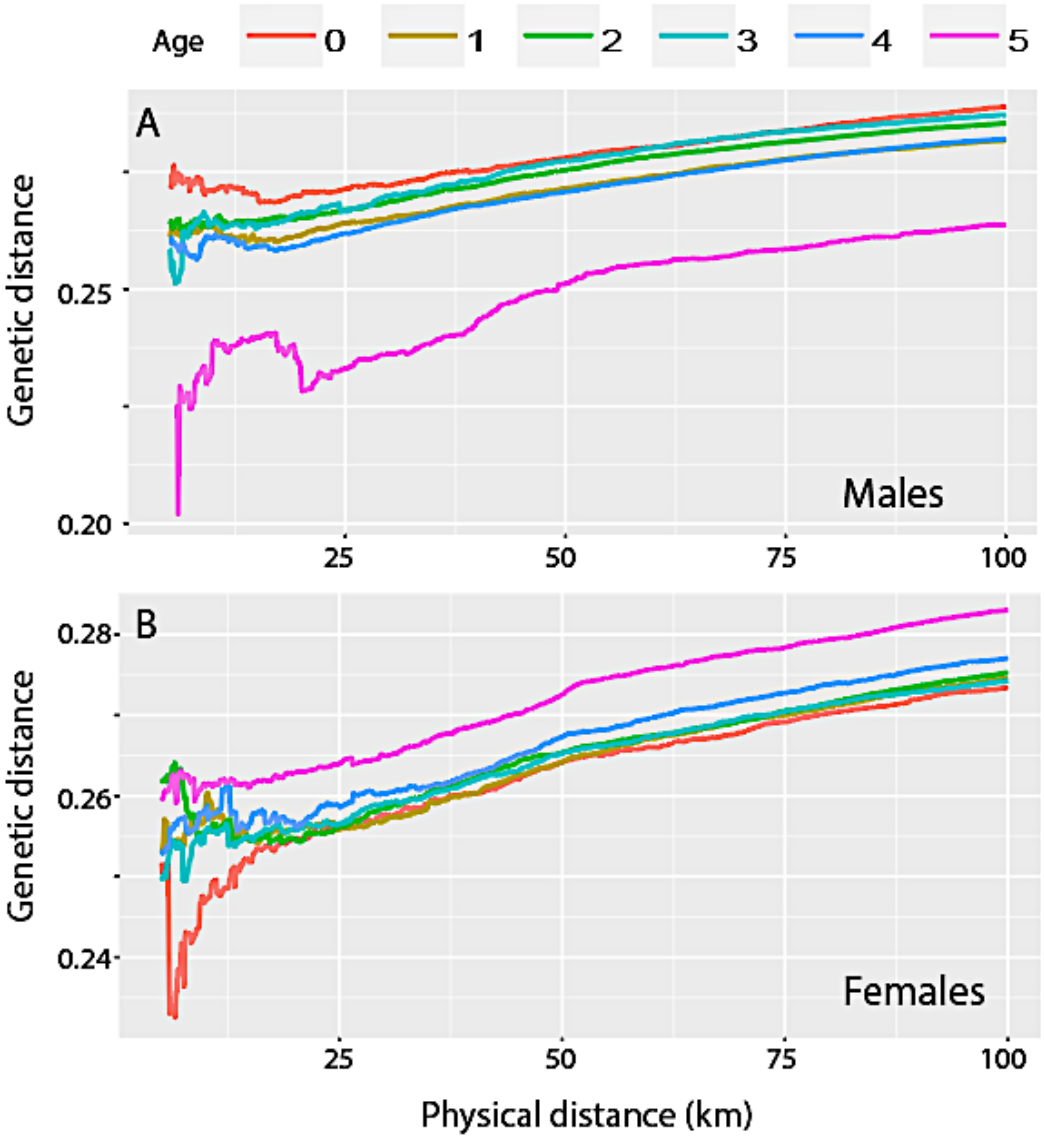

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Figure S6: **Census estimates for white-tailed deer from surveys in 1942-1946**

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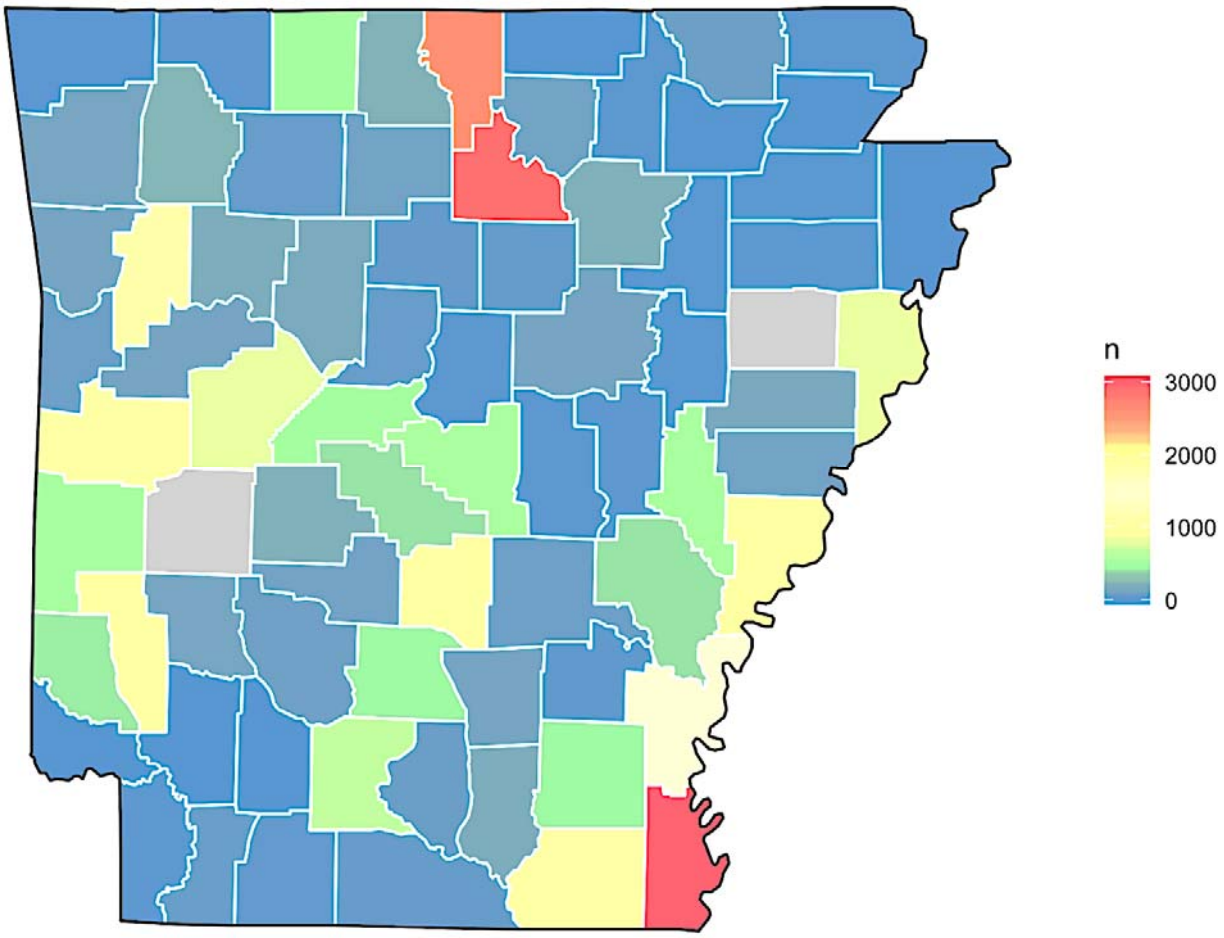

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Figure S7: Subpopulation probabilities overlain with 'deer occupied territories' circa 1942-1947 (in green). Polygons representing deer occupation were manually compiled from the Wildlife and Cover Map of Arkansas (1942-47), prepared by Arkansas Game and Fish Commission in cooperation with U. S. Fish and Wildlife Service as one aspect of a Federal Aid Project (drawn by Flaun M. Tolar). Map accessed from the University of Arkansas Library Arkansas Collection (Special Collections). A higher resolution geo-referenced version available at a later date (reproduction/ copy permissions granted by University of Arkansas Libraries).