FINE-SCALE GENETIC STRUCTURE OF EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*) AND INFLUENCES OF KINSHIP ON FEMALE SOCIALITY

by

SARA ALEXIS WATKINS

(Under the Direction of Michael J. Chamberlain)

ABSTRACT

Using 54,834 SNP variants on 414 wild turkeys I found regional variations in fine-scale genetic structure across the southeastern United States. I also used 3,498 SNP variants and GPS data on 389 turkeys to show regional variations in kin clustering among winter flocks. I found genetic relatedness was highest in a spatially fragmented region, and lowest in a population not subjected to hunting. These findings suggest fine-scale variations in genetic structure may be linked to various ecological processes such as habitat fragmentation, dispersal, and kin clustering. Additionally, I used 3,789 SNP variants and GPS data on 155 female wild turkeys to quantify social interactions and visualize social networks. Social networks and group dynamics were variable across the reproductive season. Sociality dropped significantly between the pre-laying and laying phase and contacts in all phases were predominantly between unrelated individuals.

INDEX WORDS: wild turkey, *Meleagris gallopavo silvestris*, genomics, kinship, sociality

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DEDICATION

"*We reached the old wolf in time to watch a fierce green fire dying in her eyes. I realized then, and have known ever since, that there was something new to me in those eyes—something known only to her and to the mountain. I was young then, and full of trigger-itch; I thought that because fewer wolves meant more deer, that no wolves would mean hunters' paradise. But after seeing the green fire die, I sensed that neither the wolf nor the mountain agreed with such a view*."

— Aldo Leopold, A Sand County Almanac, 1949

To the green fire. Always.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Genetic characterization of wildlife populations contributes to the fundamental knowledge of a species ecology and has direct impacts on species conservation as genetics are an important indicator of a population's viability (Frankham et al. 2002, Brown et al. 2009, Allendorf et al. 2010). In 1973, the Endangered Species Act (ESA) described the value of maintaining genetic variability in wild populations, however a lack of genetic markers and data on wild species limited its practical application in conservation and management decision-making. Modern conservation genomics is broadly defined as the application of new genomic techniques to problems in conservation biology (Allendorf et al. 2010). Recent advances in high-throughput genotyping have made discovery of single-nucleotide polymorphisms (SNPs) increasingly available for non-model species (Davey et al. 2011, Kraus et al. 2015, Supple and Shapiro 2018, Hohenlohe et al. 2021, Schweizer et al. 2021). Such advances provide improved analytical precision, and often come at a reduced cost, opening new avenues for genome-wide analysis of population genetics (Allendorf et al. 2010, Supple and Shapiro 2018, Schweizer et al. 2021).

Populations are regarded as the minimum unit for species conservation, and population genomics provide increased power to delineate populations and identify fine-scale population structure (Woodruff 2001, Allendorf et al. 2010). Scale is considered fine when the area is commensurate with the species' space use and movements, and broad when the area considered exceeds a species' dispersal limit that would be considered reasonable within a single generation

(Anderson et al. 2010, Quaglietta et al. 2013). Gene flow sculpts fine-scale genetic structure and primarily operates through the mating system and dispersal movement behavior which are governed by intrinsic biological mechanisms such as kin interaction and inbreeding avoidance (Cushman et al. 2006, Cushman and Lewis 2010, Quaglietta et al. 2013). Variations in behavioral traits and local demographics may have an additional impact on fine-scale genetic structure (Sugg et al. 1996, Storz 1999, Aspi et al. 2006, Anderson et al. 2010). An understanding of a species basic biology and demographics at the time of sampling is necessary to characterize the impacts that demographics has on fine-scale genetic structure.

At broad spatial scales, genetic structure is expected to follow concepts of isolation by distance (Wright 1943). When individuals disperse and reproduce, they contribute their genetic material to their new population, increasing the genetic similarity between populations. The greater the exchange of individuals between populations, the more that genetic similarity will increase however, this relationship is not linear (Slatkin 1987, Mills and Allendorf 1996, Johnson et al. 2010). In a model population, one individual exchanged between two populations would prevent different neutral alleles, at the same locus, from fixation (Wright 1984, Slatkin 1987, Mills and Allendorf 1996). In wild populations, social, behavioral, and demographic characteristics affect the likelihood of survival and reproduction of migrants, therefore, between 1 and 10 migrants per generation is suggested to curb fixation (Slatkin 1987, Mills and Allendorf 1996).

Genetic threats to wildlife populations include loss of genetic diversity, inbreeding during population declines and fragmentation. These threats often act synergistically with others and may have significant impacts on a population's fitness and their ability to adapt to novel conditions such as habitat loss, disease, and climate change (Hohenlohe et al. 2021). Genomics

can inform all these issues. By delineating populations and understanding the relationships among them we can identify barriers to gene flow, cryptic population structure, and more, in order to design management strategies to address these threats (Hohenlohe et al. 2021).

History, Status, and Ecology of Wild Turkeys

The wild turkey (*Meleagris gallopavo*) is an indigenous non-migratory upland game bird. Wild turkeys occupied a continuous range throughout much of North America until the early 1900's, when populations were nearly extirpated due to habitat loss and overharvest. Intensive regulatory actions, restocking efforts, and habitat restoration increased population levels and by the late 1900's turkey hunting was reestablished (Kennamer and Kennamer 1996, Allendorf et al. 2010, Eriksen et al. 2015, Supple and Shapiro 2018, Schweizer et al. 2021). Wild turkeys inhabit a diversity of vegetative communities throughout the species range, which includes all of the contiguous United States along with parts of Mexico, 6 Canadian provinces, and Hawaii (Eriksen et al. 2015). Although restoration of wild turkey populations is considered one of the most successful conservation efforts in North American history, modern age population dynamics may be facing new unknown drivers and state agencies face pressure to provide hunting opportunity (Kennamer and Kennamer 1996, Porter et al. 2011), requiring the application of modern approaches to assess and preserve the species. The eastern wild turkey (*M. g. silvestris*) is the most common and widely distributed subspecies (Eriksen et al. 2015), however there remains a paucity of information on the genetic relationships among individuals within flocks and how these relationships may influence social and movement behaviors across the subspecies range (Latch and Rhodes Jr 2005).

Historic use of genetic markers in wild turkey research and management focused on subspecies delineation (Mock et al. 2001, Mock et al. 2002, Latch 2004), hybridization of

translocated populations (Leberg 1991, Mock et al. 2001, Latch 2004, Mock et al. 2004, Latch et al. 2006*a*, Latch et al. 2006*b*), and gene flow in reintroduced populations (Leberg et al. 1994, Latch 2004, Latch and Rhodes Jr 2005, Latch et al. 2006*a*). Recent studies by Krakauer (Krakauer 2005, Krakauer 2008) used genetic data to investigate kin selection and the mating system of translocated Rio Grande wild turkeys (*M. g. intermedia*) in California. These studies used markers such as allozymes, microsatellites, amplified fragment length polymorphisms (AFLPs), mitochondrial DNA control regions (mtDNA) and cytochrome b (Latch et al. 2006*c*). Compared to modern genomic techniques, these genetic markers provide limited power for studying mating systems, relatedness, dispersal rates, and population structure (Morin et al. 2004, Allendorf et al. 2010, Lowe and Allendorf 2010, Schweizer et al. 2021).

Across the species range, aspects of social structure, characteristics of the mating system, and harvest regulations may vary and give rise to variations in genetic structure (Watts and Stokes 1971, Healy 1992). The social structure of wild turkeys is complex, and much of our current knowledge is based on visual observations. In the winter months, turkeys maintain flocks composed of multiple sibling groups of males, and groups of females with juvenile birds hatched the prior spring/summer (Watts 1969, Watts and Stokes 1971, Healy 1992). Flocks maintain strict same-sex dominance hierarchies in which an individual's status is determined in their first year of life (Watts 1969, Watts and Stokes 1971, Healy 1992). Male flocks are composed of sibling units, and remain together for life, only changing through attrition (Watts and Stokes 1971, Healy 1992). Females with mixed sex juveniles, otherwise known as a brood flock, typically combine with other brood flocks for the winter; hens that have lost their clutch or brood form broodless flocks (Watts and Stokes 1971). As the spring breeding season approaches,

female flocks shuffle into smaller harems of 2-5 individuals so that sibling hens seldom end up in the same group (Healy 1992).

In species with dominance hierarchies, social rank dictates breeding access of individuals (Robel and Ballard 1974, Foster 1983). In wild turkey the dominant male of each sibling group secures sole breeding rights to a harem of females (Watts and Stokes 1971, Healy 1992). Hamilton's inclusive fitness theory, also referred to as kin selection, suggests that individuals gain indirect fitness benefits by helping a relative secure mating opportunities (Hamilton 1964). In a population of Rio Grande wild turkey (*M. g. intermedia*) in south Texas researchers found that kin selection provided the best explanation for cooperative courtship within male coalitions (Krakauer 2005). Furthermore, Krakauer noted that these coalitions containing related males formed before adulthood and only changed through attrition, an observation discussed by other authors (Watts and Stokes 1971, Healy 1992, Krakauer 2005). Wild turkeys are unique in that their harvest season often partially or completely overlaps with their reproductive season (Chamberlain et al. 2018, Isabelle et al. 2018). Active pursuit and removal of displaying males, which may include dominant males, can alter genetic structure at the population-level through corresponding influences on density, operational sex ratios, and dispersal patterns (Robel and Ballard 1974, Nussey et al. 2005, Allendorf et al. 2008, Coster and Kovach 2012).

Sociality

Patterning genetic structure and combining it with individual movement and space use can provide valuable insights into social organization within and among flocks (Latch et al. 2006*c*). For species that are spatially structured, an understanding of animal movements is critical to describing basic species biology. Modern global positioning system (GPS) tracking devices have revolutionized inferences about animal space use and behavior (Byrne et al. 2014,

Kays et al. 2015, Walter et al. 2015). Compared to traditional tags, and other remote tracking tacks using very-high frequency (VHF), modern high-resolution GPS tags have improved power to characterize dynamic interaction between individuals (Millspaugh et al. 2004, Kays et al. 2015, Cohen et al. 2018). Conspecifics may maintain overlapping home ranges, where several individuals use the same characteristics of their habitat with or without interaction (Brown and Orians 1970, Börger et al. 2008, Rutschmann et al. 2020). Depending on temporal information, interactions can be characterized as static or dynamic (Macdonald et al. 1980). Static interactions define joint-space use and reveal the extent of home range overlap, whereas dynamic interaction consider whether 2 animals use the same space simultaneously or at different times (Macdonald et al. 1980, Doncaster 1990, Kernohan et al. 2001, Millspaugh et al. 2004, Alba-Mejia et al. 2013). Social networks can help explain conspecific interactions as well as a myriad of other behavioral activities (Li et al. 2013, Scharf et al. 2016), and may be shaped by dominance hierarchies (Noble 1939). Movements and space use of female wild turkeys during the reproductive period is highly variable (Conley et al. 2016, Bakner et al. 2019), and may have direct links to genetic structuring within flocks (Coulon et al. 2008, Cushman and Lewis 2010). Furthermore, the underlying social structure within breeding groups of females may also influence interactions, timing of breeding, and distribution of breeding females on the landscape (Robel and Ballard 1974, Foster 1983, Scharf et al. 2016), which may additionally influence genetic structure within populations. The opportunity to quantify the extent to which genetic relatedness, space use overlap, and social behavior within populations could facilitate genetic structure is rare in wild study systems (Rutschmann et al. 2020).

Using population genomics and GPS technology we were able to identify the scale on which population structure occurs, describe the spatial distribution of relatives, and describe the

role that genetic relatedness plays in hen socialization during the breeding season. In this study, we collected data from 4 regions in the southeastern United States occurring in 3 states: Georgia, Louisiana, and South Carolina. Habitat, land management activities, and hunting regulations varied across regions. Chapter 2 describes broad and fine-scale genetic structuring of winter flocks and describes regional variations in the spatial distribution of relatives. Chapter 3 quantifies dynamic social interactions of female wild turkeys during the reproductive season and investigates the influence of kinship on social group membership. The final chapter provides conclusions and management implications.

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CHAPTER 2

FINE-SCALE GENETIC STRUCTURING IN WINTER FLOCKS OF EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*)[1]

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Abstract

Genetic characterization and delineation of local populations contribute to the knowledge of species ecology and are essential to understand how behavioral and ecological processes shape the spatial distribution of genetic variation. The eastern wild turkey (*Meleagris gallopavo silvestris*) is the most common and widely distributed subspecies of wild turkey, however there is a paucity of information on population genetics and the genetic relationships among individuals within flocks. Advances in population genomics now provide us increased power to delineate populations and identify the scales on which population structure occurs. We used a population genomics approach to investigate genetic structuring of 414 wild turkeys in Louisiana, Georgia, and South Carolina. We found that at broad spatial scales, turkeys exhibited clustering suggestive of 4 distinct populations; 1 each in Georgia and South Carolina, and 2 in Louisiana. Average relatedness within winter flocks was highest in southeast Louisiana (r = 0.14) and lowest in South Carolina (r = 0.03), a population not subjected to hunting. When we investigated the spatial structuring of relatives, we found the average geographic distance between female relatives was higher than distances between male relatives at all sites except in South Carolina. Our findings suggest, on a fine-scale, variations in genetic structure may be linked to various ecological processes, such as habitat fragmentation, dispersal, and kin clustering.

Introduction

Genetic characterization of populations not only contributes to the fundamental knowledge of a species ecology, but genetic aspects of species conservation are also important indicators of population viability (Frankham et al. 2002, Brown et al. 2009, Allendorf et al. 2010). The 1973 Endangered Species Act (ESA) directly emphasized the value of maintaining genetic variability in wild populations, but the lack of genetic markers and data on wild species created barriers to practical application in conservation and management decision-making. Recent advances in Next Generation Sequencing (NGS) have made discovery of single-nucleotide polymorphisms (SNPs) readily available for non-model organisms through high-throughput genotyping (Morin et al. 2004, Davey et al. 2011, Kraus et al. 2015). Specifically, restriction site-associated DNA sequencing (RADseq) identifies thousands of genetic markers across the genome, and is particularly useful for population genetic studies on species with limited existing sequence data (Davey and Blaxter 2010, Davey et al. 2011). When compared to traditional markers, these contemporary markers provide increased power to study mating systems, relatedness, dispersal rates, and population structure (Morin et al. 2004, Allendorf et al. 2010, Lowe and Allendorf 2010).

Behavioral, ecological, and evolutionary processes shape the geographic distribution of genetic variation (Slatkin 1987, Sugg et al. 1996, Storz 1999, Costello et al. 2008, Coster and Kovach 2012). Sewall Wright (1943) demonstrated that genetic structuring on broad spatial scales follows concepts of isolation by distance, and that genetic variation can be partitioned to reflect population structure (1984). Gene flow, or a lack thereof, shapes broad and fine-scale genetic structure through dispersal behaviors and the mating system. Among the most well documented influences on gene flow are natural and anthropogenic landscape barriers (Cushman

et al. 2006, Keyghobadi 2007, Hawkes 2009, Anderson et al. 2010), but genetic structuring also occurs in the absence of such barriers (Aspi et al. 2006). Most notably, local variations in mating systems, social structure, and harvest pressures are known to sculpt fine-scale genetic structuring of populations (Mills and Allendorf 1996, Nussey et al. 2005, Allendorf et al. 2008, Cushman and Lewis 2010, Quaglietta et al. 2013).

Wild turkeys (*Meleagris gallopavo*) inhabit a diversity of vegetative communities throughout the species range, which includes all of the contiguous United States along with parts of Mexico, 6 Canadian provinces, and Hawaii (Eriksen et al. 2015). Across the species range, aspects of social structure, characteristics of the mating system, and harvest regulations may vary and give rise to variations in genetic structure (Watts and Stokes 1971, Healy 1992). Most previous work on genetics within populations of wild turkeys was directed at subspecies delineation, hybridization of translocated populations, and gene flow in reintroduced populations (Mock et al. 2002, Latch et al. 2006*b*). Furthermore, these works were limited to use of molecular markers such as allozymes, microsatellites, amplified fragment length polymorphisms (AFLPs), mitochondrial DNA control regions (mtDNA) and cytochrome b, which have reduced power compared to modern genomic techniques (Latch et al. 2006*a*, Latch et al. 2006*b*, Allendorf et al. 2010, Schweizer et al. 2021). The eastern wild turkey (*M. g. silvestris*) is the most common and widely distributed subspecies (Eriksen et al. 2015), but there is a paucity of information on the genetic relationships among individuals within flocks and how these relationships may influence population genetics across the subspecies range.

Current knowledge of winter flock structure is based entirely on visual observations. During winter, wild turkeys maintain flocks composed of multiple sibling groups of males and sibling groups of females with juvenile birds hatched the prior spring/summer (Watts and Stokes

1971, Healy 1992). As spring approaches, wild turkeys transition from winter flocks to harems of females that are associated with a small group of males that may, or may not, be related (Watts and Stokes 1971, Krakauer 2005, Krakauer 2008). Studies utilizing allozymes, microsatellites, and control region sequences have shown that timing and method of sampling causes discrepancies in estimates of local genetic structure (Leberg 1991, Rhodes Jr et al. 1995, Boone and Rhodes Jr 1996, Latch and Rhodes Jr 2005). Because samples collected in winter are from discrete flocks, they provide an appropriate sampling unit to identify the hierarchical scale at which genetic differentiation occurs, and can lead to an improved understanding of social and behavioral dynamics (Rhodes Jr et al. 1995, Boone and Rhodes Jr 1996, Latch and Rhodes Jr 2005).

Our objectives were to describe the genetic characterizations and structure of winter flocks of wild turkeys in the southeastern United States, and to investigate whether genetic structuring occurred at fine spatial scales. We suspected that examining variations in fine-scale genetic structure would fill knowledge gaps in the basic species ecology, while also providing insight into gene flow and social structuring of winter flocks. Herein we used a model-based maximum likelihood framework and non-parametric principal components analysis to look for genetic structuring across and within 4 regions of the eastern wild turkey's range. We hypothesized that genetic structuring would follow basic isolation-by-distance principals at broad spatial scales but exhibit regional variations in fine-scale genetic structure. We also calculated genetic relatedness and pairwise geographical distances of relatives to examine local spatial structuring of relatives. Based on historic visual observations of wild turkeys detailed in Watts and Stokes (1971), we expected winter flocks of adult males and flocks of adult females with mixed-sex juveniles to have elevated relatedness compared to other flocks, due to the assumption

that male coalitions are influenced by kin selection (Hamilton 1964, Krakauer 2005) and that brood flocks remain together for the first winter (Krakauer 2005).

Study Area

We used data from 8 sites in the Southeastern United States (Figure 2.1) within the states of Georgia, Louisiana, and South Carolina. Specifically, we used data from 3 sites located within the Piedmont region of Georgia, including B.F. Grant Wildlife Management Area (BFG), Cedar Creek Wildlife Management Area (CCWMA), and Piedmont National Wildlife Refuge (PNWR). Cedar Creek was 15,303 ha located in Jones, Jasper, and Putnam counties. Cedar Creek was owned by the U.S. Forest Service (part of Chattahoochee-Oconee National Forest) and managed in partnership with Georgia Department of Natural Resources – Wildlife Resources Division (GADNR). Landscape composition at CCWMA was predominantly upland loblolly pine stands (*Pinus taeda*), mixed pine-hardwood forests, and hardwood lowlands dominated by oaks (*Quercus spp*.), sweetgum (*Liquidambar styraciflua*.), and hickories (*Carya spp*.). Typical management regimes involved broad-scale prescribed burns during the dormant season on 3–5-year intervals. B.F. Grant WMA was 4,856 ha located in Morgan and Putnam counties and was owned by the Daniel B. Warnell School of Forestry and Natural Resources at the University of Georgia. In cooperation with the GADNR, prescribed fire was used as the primary vegetation management tool. B.F. Grant consisted of loblolly pine stands, agricultural fields, mixed pine-hardwood forest, and hardwood bottoms of similar composition to CCWMA. Piedmont National Wildlife refuge was 14,163 ha located in Jones and Jasper counties. Landscape composition was predominantly loblolly pine uplands with hardwoods found along riparian areas. Habitat management was focused on needs of the federally endangered red-cockaded woodpecker

(*Dryobates borealis*) and included prescribed fire and thinning. For a detailed description of site condition on BFG and CCWMA, see Wakefield et al. (2020).

We used data from 2 sites in western Louisiana (WLA), including Kisatchie National Forest (KNF) and Fort Polk Wildlife Management Area (FPWMA). The KNF was owned and managed by the United States Forest Service (USFS) and FPWMA was jointly owned by the USFS and the United States Army. Both sites were composed of pine (*Pinus* spp.)-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility rights-of-way, and forest roads distributed throughout. Primary overstory species included longleaf pine (*Pinus palustris*), loblolly pine, oaks, hickories, and red maple (*Acer rubrum*). For a detailed description of site conditions on KNFs and FPWMA, see Yeldell et al. (2017*a*, 2017*b*).

We used data from a broad suite (~ 2900 ha) of private and public lands in southeastern Louisiana (SELA), including Sandy Hollow WMA (1880 ha) in Tangipahoa and Washington Parishes. The region was composed of rolling hills with hardwood riparian zones interspersed with young longleaf pine plantations. Agricultural production included grazing and row crops were the dominant land use. For a detailed description of Sandy Hollow WMA, see Duguay et al. (2017).

Lastly, we used data from South Carolina collected on the Savannah River Site (SRS). The SRS was a 78,000-ha former nuclear production facility located in Aiken, Barnwell, and Allendale counties and was owned by the United States Department of Energy. Vegetation communities ranged from sandhills in the xeric uplands to bottomland or swamp forests in low-elevation areas that were subjected to periodic flooding. Management activities included timber production and prescribed fire. For detailed description of site conditions on SRS see Wightman et al. (2019).

Methods

General Methodology

In SELA, WLA, and Piedmont, turkeys were captured from January-March of 2020 and January-March of 2021. At SRS, turkeys were captured from January-March and December of 2020 and from January-March of 2021. Turkeys were captured with rocket nets, or similar methods, on all sites. All birds were sexed and aged using the presence (adult) or absence (juvenile) of barring on the ninth and tenth primary feathers (Pelham and Dickson 1992). Each bird was uniquely marked with an aluminum leg band (National Band and Tag company, Newpor, Kentucky, USA). Select individuals were fitted with a backpack style GPS transmitter that was remotely downloadable, mortality-sensitive, and equipped with VHF capabilities. For genomic analysis, a blood sample was collected from the brachial vein of each individual. The blood was immediately transferred to a microcapillary tube and combined with lysis buffer (100mM Tris, 100 mM EDTA, 10 mM NaCl, 2% SDS). The Tris-EDTA buffer stabilized the solution and allowed for room-temperature storage and shipment of samples. Birds were released at the capture site after processing. Capture, handling, and marking procedures are approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol #A2019 01-025-R2 and A2020 06-018-R1) and Louisiana State University (Protocol #A2018-13).

Reduced Representation Sequencing and Data Processing

The DNA was extracted from blood samples at Princeton University using Qiagen Dneasy blood and tissue kits (Qiagen, Maryland, USA) following manufacturer protocols. We sequenced data using a restriction site-associated DNA sequencing (RADseq) method (Ali et al. 2016) and cleaned using STACKS v2 (Catchen et al. 2013). We determined single-nucleotide polymorphism (SNP) variants for each genome and made a catalog of all variants detected, at

which point we genotyped individuals for SNPs in the catalog. We pruned the initial set of loci using PLINK v1.9 (Purcell et al. 2007). For all analyses, we followed a multi-step filtering process. After initially filtering out loci with >10% missing data (--geno 0.1) and calculating the remaining missing data per sample, there was an obvious tail of low-quality samples, so we removed samples that had >15% missing data (--mind 0.15). We then recalculated missing data per loci. Most loci had low missing data, so we removed a small tail of low-quality loci that had >5% missing data (--geno 0.05). This left the data set with 358,094 variants for 414 individuals.

For the population admixture and principal component analysis (see below), we required a statistically unlinked set of SNP loci, hereafter the neutral SNP set. We filtered for linkage disequilibrium (LD) in PLINK using the flag and parameters –indep-pairwise 50 5 0.5. We then filtered SNPs to retain those in Hardy-Weinberg equilibrium (--hw 0.001) and had minor allele frequencies (MAF) below 0.05 (--maf 0.05). For calculating genetic relatedness, the neutral SNP set followed the same LD and HW filtering but was filtered for MAF below 0.40 (--maf 0.40).

Modeling Population Structure and Relatedness

We used a model-based maximum-likelihood framework (*ADMIXTURE* v1.3.0: Alexander et al 2009) to describe population structure within and across study regions (Georgia, South Carolina, Western Louisiana, Southeastern Louisiana). Admixture estimates the true number of genetic populations (clusters, *K)* using a cross validation (CV) to estimate the most accurate *K*. The best fit *K* is considered to have the lowest CV score (Alexander et al. 2009). Because population structure analyses are sensitive to MAF thresholds, we followed practices outlined by Linck and Battey (2019) by duplicating the population structure analysis with a principal components (PCA) analysis. We used an individual-based PCA with data from all 4 regions to explore the orientation and clustering of individuals among regions. We also

conducted region-specific PCAs to explore the orientation and clustering of individuals among sites and individual flocks within each region. We calculated eigenvalues from a matrix of genetic distance between individuals (PLINK, --distance-matrix) using the *cmdscale* function in R stats v3.6.2. We extracted the top 8 principal components and visualized the top 2 in R using the package *ggplot2* (Wickham 2016).

We calculated the pairwise relatedness of individuals using the coancestry function in the package *related* (Pew et al. 2015) in R v3.6.2. The package provided a suite of relatedness estimators, and to determine the estimator that best suited our dataset, we simulated 100 pairs of individuals for each degree of relatedness. We then calculated the correlation coefficients between the observed and expected relatedness values for each estimator, and selected the relatedness estimator that resulted in the highest correlation coefficient. Simulations revealed that the dyad maximum likelihood estimator (dyadml) and the Lynch and Ritland estimator (lynchrd) had the highest correlation coefficients in all regions (Lynch and Ritland 1999, Milligan 2003). We selected dyadml because it is constrained so that minimum relatedness is always 0 and pairwise estimates reflect biologically interpretable relationships between individuals (Milligan 2003). We binned relatedness coefficients into 4 categories: unrelated (UR) < 0.0625, 3^{rd}-order ≥ 0.0625 & < 0.1875, 2^{nd}-order ≥ 0.1875 & < 0.3125, and 1^{st}-order ≥ 0.3125. First-order relatives typically reflect parent-offspring or full-siblings. Half-siblings, grandparents, cases of extra-pair paternity (EPP) by related males, and quasi-parasitism (QP) from a related female typically fall within the second order. Extra-pair paternity is the result of copulation between a female and multiple male. Quasi-parasitism occurs when a female lays an egg in another female's nest and that egg is fertilized by a male already represented at the parasitized nest (Griffith et al. 2004).

The third order reflected distant relatives including but not limited to cousins, great grandparents, and many combinations of EPP and QP.

We binned each winter flock into one of 8 categories based on their sex and age composition: [1] adult females, [2] adult females with mixed-sex juveniles, [3] juvenile males, [4] juvenile females, [5] adult males, [6] mixed-sex adults, [7] mixed-sex adults and juveniles, and [8] mixed-age males. We calculated and compared the average relatedness of each flock type among and within regions to look for differences in winter flock composition. Additionally, we calculated pairwise geographical distances between individuals within each region as Euclidean distances (ED), which were the shortest straight-line distance according to the ellipsoid method using the *geosphere* v1.5-14 package in R (Hijmans et al. 2017). We compared the average pairwise geographic distance among the orders of relatives both among and within regions to look at regional and local spatial structuring of relatives.

Results

Across all 4 regions, 481 wild turkeys (277 females, 196 males and 6 unknown sex juveniles) were captured and blood sampled. Of these 481 samples, 424 were genotyped and after the first round of filtering, we retained 414 individuals and 358,094 SNP variants.

Broad-scale Population Structure

Filtering for a neutral SNP set and a MAF below 0.05 resulted in me retaining 54,834 variants and 414 individuals. A PCA of 414 individuals from all 4 regions identified 4 genetic clusters with individuals from each region generally forming a single cluster (Figure 2.2). The first 2 principal components (PCs) explained 6.5% and 4.4% of the total genotypic variation, with individuals in the Piedmont and SRS clusters orienting closer to one another than to SELA or WLA. These locations were also geographically more proximate. Samples assigned to the

Piedmont and SRS clustered with considerable overlap between individuals within each region, except for a single cluster of birds in the Piedmont. Principal component 2 (PC2) separated SELA at a greater distance from WLA than one would expect based on their relative geographic proximity. The degree of overlap in WLA varied, as adjacent sites within the region overlapped but sites separated by >30 km did not.

In the *ADMIXTURE* analysis, when 4 populations were assumed ($K = 4$) assignments to inferred clusters corresponded to *a priori* regional designations (Figure 2.3), which was similar to clustering observed in the PCA. Examination of the cross-validation results to select the *K*-value that best represented the dataset produced a double minimum CV score (cverr), likely a result of elevated relatedness within flocks in SELA (see below). Across all investigated *K*-values SRS identified as a single population, whereas the first regional subdivision occurred in SELA at K=5, followed by a subdivision in Piedmont at K=6. Cross validation identified 8 (K=8) as the optimal number of clusters. At K=8, SRS remained a single population, Piedmont and WLA had 2 subdivisions each and SELA had 3.

Fine-scale Population Structure

In our analysis of 104 individuals from SRS, there was no apparent population structuring. The first 2 PCs explained 3.02% and 2.72% of the variation and did not reveal clustering at any level (Figure 2.4a). Additionally, the CV score in *ADMIXTURE* indicated SRS was a single cluster, and even at K=2, > 75% of individuals were similarly admixed (Figure 2.4b).

Principal component analysis of 81 turkeys in the Piedmont revealed minimal clustering with the first 2 PCs explaining 6.86% and 3.09% of the variation (Figure 2.5). One breakout cluster was assigned *a priori* to CC (flock CC 57), but the morning following capture most

(93%) of the flock moved west 5 miles to the Piedmont National Wildlife Refuge. *ADMIXTURE* generally agreed with the PCA and optimized when 2 populations were assumed (*K*=2; Figure 2.6a). The 2 sites in this region (CC, BFG) were identified as a single population, and the breakout population was comprised of flock members from CC 57. The inclusion of 18 hunter harvest samples collected from > 10km from either site did not change the optimal *K*-value, nor did it introduce clustering to the PCA.

Cross-validation in *ADMIXTURE* of 93 individuals from WLA suggested 2 populations (*K*=2; Figure 2.7a). The southern sites of KNF-Vernon and FPWMA clustered with considerable overlap in the PCA (Figure 2.7b) and were identified as a single population, whereas the northern site (KNF-Kisatchie) identified as a population consisting of mostly admixed individuals. Peason Ridge WMA (PRWMA) lies in between the northern and southern clusters, separated by a geographic distance of ~27 km and ~29km, respectively. Individuals from PRWMA had similar admixture levels to the southern sites (Figure 2.7a) but formed a distinct outgroup with PC2 separating them from the southern cluster (Figure 2.7b).

In southeast Louisiana, across 118 individuals there was strong hierarchical patterns of genetic structuring where sites exhibited consistent differentiation, whereas neighboring trap locations showed more subtle differentiation (Figure 2.8a). Because site assignments were less clear, we faceted *ADMIXTURE* results at the flock level (Figure 2.8a). Cross-validation suggested 3 populations (*K*=3, cverr = 0.394) within this region with an additional minimum at *K*=5 (cverr = 0.387; Figure 2.8b). This unique ‘w’ pattern suggested sites and flocks in SELA contained many related individuals (Figure 2.8b). In a PCA, the first 2 PCs explained 6.84% and 5.38% of the variation and produced 3 clusters with varying levels of overlap (Figure 2.9). In the PCA and across all *K*-values, there was a distinct population of birds within the Miller flock at

the Sandy Hollow site. This flock clustered with high overlap in the PCA and was always identified as a distinct, non-admixed population in *ADMIXTURE*. At K=3, Tchefuncte River and the Miller flock in Sandy Hollow were generally distinct, non-admixed populations (Figure 2.8a). The third distinct population contained individuals in Amite and Kentwood (J.Alston-20A, J.Alston-20B, Phelps). One flock in Amite (J.Alston-20C), 2 Kentwood (McCabe, Phelps), and 4 Sandy Hollow (B.Hayden-A/B, K.Stevens, Dan.Miller) shared similar levels of admixture (Figure 2.8a).

Genetic Relatedness of Winter Flocks

We retained 389 individuals and 3,498 variants for calculating genetic relatedness (r-coefficient) among and within flocks in each region. Mean relatedness within winter flocks differed among regions ($F_{3,1038} = 23.267$, $P < 0.001$; Figure 2.10a). A Tukey post-hoc test revealed pairwise differences between all regions except for WLA and Piedmont ($P = 0.809$; Figure 2.10b). Flocks in SELA had an average r-coefficient of 0.143, indicating most flock members were at least 3rd-order relatives, whereas flocks on SRS had an r-coefficient of 0.0306, suggesting that most flock members were either not related or distantly related.

An ANOVA allowing the interaction between region and flock type revealed mean relatedness of winter flocks among regions was influenced by flock type (Table 2.1). Among regions, we found a difference in mean relatedness in flock types 2 ($F_{3,663} = 15.96$, $P < 0.001$) and 5 ($F_{3,61} = 9.962$, $P < 0.001$). In flocks containing adult females with mixed-sex juveniles, relatedness was lower on SRS than all other regions (Figure 2.11a). Among 149 pairwise comparisons average relatedness was 0.024, indicating most flock members were unrelated (Appendix A, Table 1). In flocks of adult males, SELA had higher relatedness than all other

regions (Figure 2.11b). Among 21 pairwise comparisons within flocks of adult males in SELA average relatedness was 0.274, and 57% were 1st or 2nd-order relatives (Appendix A, Table 1).

When we calculated relatedness for all possible dyads within a region, we did not see the trend of average relatedness change among regions. Relatedness in SELA remained higher, and SRS remained lower than all other regions ($F_{3,15345}$=32.46, $P < 0.001$).

After filtering, we retained 86 individuals from 16 winter flocks at SRS. Flocks of adult females with mixed-sex juveniles (n=5) were most frequently captured along with flocks of adult males 5 (n=5) and adult females (n=4). Regardless of flock type, 94% individuals within flocks at SRS were unrelated ($r < 0.0625$) and we found no significant difference in average relatedness ($F_{4,223} = 1.793$, $P > 0.05$) (Appendix A, Table 1).

After filtering, we retained 69 individuals from 11 winter flocks in the Piedmont region, and noted that 74% of individuals within flocks were unrelated ($r < 0.0625$). Flocks of adult females with mixed-sex juveniles were most frequently captured ($n = 5$) and these flocks had higher relatedness compared to other flock types in the Piedmont ($F_{4,228} = 3.045$, $P = 0.018$). Low sample sizes for other flock types prevented meaningful inferences (Appendix A, Table 1).

After filtering, we retained 85 individuals from 21 winter flocks in WLA. Flocks of adult males were most commonly captured ($n = 7$) followed by flocks of adult females with mixed-sex juveniles ($n = 6$). Pairwise comparisons within each flock were low and created data distributions that were not appropriate for parametric statistical tests.

After filtering, we retained 108 individuals from 16 winter flocks in SELA. Flocks of adult females with mixed sex juveniles were most commonly captured ($n = 6$) followed by flocks of mixed-age males ($n = 4$). Average relatedness within flocks in SELA was 31-78% higher than other regions ($F_{3,1038} = 23.267$, $P < 0.001$; Figure 2.10a) with all flock types exceeding the

unrelated threshold ($r > 0.0625$, Figure 2.12a). In 12 of 16 flocks, ≥25% of the flock members were related at the 1st or 2nd-order.

Spatial Structuring of Relatives

When we included dyads of all ages/sex, there was no statistical difference of geographic distances among regions for 1st and 2nd order relatives (Table 2.2). Across all regions except SRS, we observed greater average distances between 1st and 2nd order female relatives than male relatives (Table 2.3).

Specific to adults, in Piedmont, WLA, and all but one dyad in SELA, we noted that all 1st-order adult males were members of the same winter flock, whereas at SRS only 50% of adult males classified as 1st-order relatives were in versus out of winter flocks. In female dyads, there was a 50:50 split of 1st-order relatives in versus out of winter flocks at SRS and Piedmont. In WLA and SELA, 1st-order female relatives were within the same winter flock 73% and 87% of the time, respectively. One hundred percent of male-female relatives ($r > 0.0625$) at SRS and Piedmont were not within the same flock, whereas in WLA 97.7% were not within the same flock. In SELA, 100% of 1st-order male-female relatives were within the same winter flock, whereas 97.6% of 2nd and 3rd-order male-female relatives were not in the same winter flock.

Discussion

Genetic characterization of populations contributes to the fundamental knowledge of species ecology and is essential to understand how behavioral and ecological processes shape the geographic distribution of genetic variation (Slatkin 1987, Sugg et al. 1996). Populations are typically regarded as the minimum unit for species conservation, and population genomics provide increased power to delineate populations and identify fine-scale population structure (Woodruff 2001, Allendorf et al. 2010). Previous genomic work on wild turkeys relied on

molecular markers that provide reduced power for quantifying population differentiation and fine-scale structure within populations when compared to contemporary RADseq approaches (Morin et al. 2004, Latch et al. 2006*b*, Davey et al. 2011). We used a pool of 54,834 variants across 414 individual wild turkeys to determine that population structure varied at relatively fine geographic scales. Scale is considered fine when the area is commensurate with the species' space use and movements, but broad at regional or state levels (Anderson et al. 2010, Quaglietta et al. 2013). Gene flow sculpts fine-scale genetic structure. Gene flow primarily operates through the mating system and dispersal movement behavior which are governed by intrinsic biological mechanisms such as kin interaction and inbreeding avoidance (Cushman and Lewis 2010, Quaglietta et al. 2013). Though a major factor influencing movement behavior is landscape barriers, genetic structuring also occurs in the absence of such barriers (Aspi et al. 2006). Previous authors have noted that variation in behavioral traits and demographics may have additional consequences for shaping fine-scale genetic structure within populations (Sugg et al. 1996, Storz 1999, Anderson et al. 2010). Current knowledge of flock demographics in the eastern subspecies of wild turkey is limited to visual observations. Describing flock demographics, specifically the local spatial structuring of relatives, at the time of sampling, helped characterize its impact on fine-scale genetic structure.

At broad spatial scales, genetic structuring is expected to follow concepts of isolation by distance (Wright 1943). We found that wild turkeys across our study regions exhibited clustering suggestive of 4 distinct populations. Generally, turkeys clustered corresponding to their a priori regional designations. We noted that the SRS and Piedmonts clusters were genetically more similar to each other than they were to populations in Louisiana, which is not surprising given their relative geographic distances (177km between SRS and Piedmont). Conversely, the

Louisiana clusters (WLA and SELA) were separated by an average of 264 km, but exhibited a greater degree of separation than we expected given their proximity. Contemporary literature has noted substantive influences of natural and anthropogenic landscape barriers, such as water bodies and highway systems, on gene flow (Stow et al. 2001, Keyghobadi 2007, Coster and Kovach 2012). We note that wild turkey populations in western and southeastern Louisiana are separated by barriers capable of contributing to restricted or frustrated dispersal and a lack of gene flow, including the Mississippi River, Interstates 55 and 49, and the city of Baton Rouge.

Delineation of naturally occurring populations is the first step in inferring fine-scale population structure. When individuals disperse and reproduce they contribute genetic material to their new population, increasing genetic similarity between populations. The greater the exchange of individuals between populations, the more that genetic similarity will increase. However, this relationship is not linear and only a few individuals that move between populations in each generation is often sufficient to stump effects of genetic drift on gene frequency (Slatkin 1987, Mills and Allendorf 1996, Johnson et al. 2010, Quaglietta et al. 2013).

In the Piedmont and WLA, we found minimal fine-scale clustering of individuals. Geographic distances can explain a large proportion of genetic variance observed in a PCA where winter flocks separated by < 15 km clustered with considerable overlap. Despite > 30 km between the northern (KNF-Kisatchie) and southern sites (KNF-Vernon & FPWMA) of WLA, there was evidence of gene flow. Individuals from the northern region had distinct levels of admixture but most shared 30% of ancestry proportions with the southern region. Recent versus historic gene flow can be difficult to differentiate. If a population's isolation is recent, they might appear to have gene flow even if they are totally isolated because molecular differences take time to accumulate (Oyler-McCance and Leberg 2005). Continued monitoring of this population and

future work studying runs of homozygosity (ROH) could help determine if the genetic admixture observed in WLA was a relic of historic gene flow or if these populations were in the isolation process (Hohenlohe et al. 2021).

A popular theory in conservation genetics is that one migrant individual per local population per generation (OMPG) is sufficient to obscure the disruptive effects of genetic drift (Wright 1943, Spieth 1974, Allendorf 1983, Mills and Allendorf 1996). Mills and Allendorf (1996) highlighted violations of OMPG frequently made by natural populations due to variations in mating systems and social structure, and concluded that a minimum of 1 and a maximum of 10 migrants per generation are an appropriate threshold for natural populations. In the Piedmont, winter flocks across two sites were separated by 1-35 km yet 14/15 flocks identified as belonging to the same breeding group. Further data exploration revealed 6 high-order dyads contained a representative from each study site. The exchange and subsequent successful reproduction of individuals between populations has decreased the genetic variation between these regions in a manner concordant with the thresholds suggested by Mills and Allendorf (1996).

Hunting and harvest can alter genetic structure at the population-level through corresponding influences on density, operational sex ratios, and dispersal patterns (Nussey et al. 2005, Allendorf et al. 2010, Coster and Kovach 2012). Wild turkeys on SRS were not exposed to hunting during our study, and broad areas of the site have not been hunted for decades (Moore et al. 2005). Boone and Rhodes (1996) characterized fine-scale genetic composition of wild turkey flocks on SRS, and concluded that gene flow amongst flocks in close proximity was minimal. Conversely, we found that among 24 winter flocks on SRS separated by 0.5 to 22.5 km, there was no evidence of population subdivision. Such homogenized genetic structure is facilitated by movement of individuals between flocks with subsequent reproduction by these same individuals

(Slatkin 1987). Therefore, our findings suggest that gene flow is uninhibited on SRS, resulting in a lack of spatially distinct genetic structuring.

Although winter flock composition at SRS was similar to other regions, we observed that average relatedness within winter flocks was 63-78% lower. We hypothesized that winter flocks that contained adult females and mixed-sex juveniles would exhibit higher mean relatedness compared to other flock types, due to the assumption that these flocks were at least partially comprised of adult females with their broods. Our data supported this hypothesis in all regions except SRS, where mean relatedness of these flocks was 76-83% lower. This finding suggests there was increased natal dispersal at SRS, in which juveniles likely dispersed from brood flocks prior to the formation of winter flocks. Mock et al. (2002) noted that in the absence of human intervention, dispersal in wild turkeys was most likely dominated by juvenile females (Ellis and Lewis 1967, Eaton et al. 1976, Exum et al. 1985), a hypothesis supported by Greenwood's (1980) theory that females are the primary disperser in many avian systems. Clearly, dispersal from flocks containing close relatives (e.g., parents, direct siblings) prior to winter flock formation would contribute to a lack of fine-scale spatial genetic structuring similar to what we observed on SRS.

Hamilton's inclusive fitness theory, also referred to as the concept of kin selection, suggests that individuals gain indirect fitness benefits by helping a relative secure mating opportunities (Hamilton 1964). Krakauer (2005) found that kin selection provided the best explanation for cooperative courtship within male coalitions of wild turkeys. Furthermore, Krakauer (2005) noted that these coalitions containing related males formed before adulthood, and only changed through attrition, an observation also discussed by other authors (Watts and Stokes 1971, Healy 1992). Based on these observations, we expected dyads of closely related

adult males (male coalitions) to exhibit spatial clustering, or in other words, be located close to each other within their home ranges. However, when considering the spatial distribution of 1st and 2nd-order relatives, SRS was the only region in which male coalitions exhibited higher average geographic distances than female dyads. In fact, at SRS we noted that 50% of the time, male coalitions did not contain any 1st or 2nd order relatives, and the average distance between these coalitions was 3 times higher than that of female dyads. Conversely, across regions we observed that 50-87% of females classified as 1st-order relatives were within the same winter flocks, with this percentage noticeably higher in Louisiana. We also observed that adult males and adult females were unlikely to spend time in the same winter flock, consistent with previous studies suggesting that such segregation likely resulted from inbreeding avoidance (Greenwood 1980, Pusey 1987, Sugg et al. 1996, Costello et al. 2008). However, we found that in SELA, male and female 1st order relatives were always in the same winter flocks. Constricted spatial structuring of related individuals may increase certain gene frequencies and enhance genetic differentiation, due to genetic drift, among flocks, giving rise to localized genetic differentiation (Healy 1992, Kennamer et al. 1992, Boone and Rhodes Jr 1996).

Fine-scale population subdivision can be of conservation concern, as it is known to reduce effective population size (Aspi et al. 2006, Keyghobadi 2007). Likewise, natural and anthropogenic landscape features that alter the distribution and quality of habitat patches influences dispersal behavior and gene flow (Hawkes 2009). We observed a high degree of population subdivision in SELA, both among capture sites and flocks separated by an average 18 km. This result was unexpected given the vagility of wild turkeys, which facilitate gene flow and reduce genetic substructure at this distance. Leberg (1991) reported that genetic differentiation among populations of wild turkeys in fragmented landscapes was greater than in

more contiguous landscapes. We speculate that the lack of evidence for dispersal in SELA may be related to fragmentation of vegetative communities suitable for wild turkeys and may be a key factor in the population subdivision of this region.

Although landscape conditions affect gene flow, socially mediated constraints on gene flow could also have influenced our results, as social structuring of populations has been shown to promote genetic subdivision through its effect on mating and dispersal behaviors (Chesser 1991*a*, Chesser 1991*b*, Storz 1999, Cushman and Lewis 2010). Chesser (1991*a*, 1991*b*) mathematically demonstrated that social organization and breeding patterns have important consequences for the apportionment of genetic variance. Strong site fidelity, often exhibited by one sex, can reduce gene flow and give rise to spatial genetic structure in the absence of geographic barriers (Chesser 1991*a*, Jahner et al. 2016). Furthermore, the potential for kin-selection, which is known to function in the mating system of male wild turkeys (Watts 1969, Watts and Stokes 1971, Krakauer 2005, Krakauer 2008) can enhance drift in structured populations and give rise to fine-scale spatial genetic structure (Segelbacher et al. 2003, Johnson et al. 2004). Jahner et al. (2016) found elevated relatedness within sage-grouse leks and suspected that reproductive skew, where few males participate in most successful matings as in kin-selection, created fine-scale genetic structure among lek complexes. Although it is difficult to directly account for the effects of reproductive skew (Sugg et al. 1996), our observations of limited spatial distribution of close relatives in SELA suggests that kin clustering could be preventing complete admixture of genes among groups.

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Table 2.1: Results from an analysis of variance testing for differences among mean relatedness values of eastern wild turkeys (*Meleagris gallopavo silvestris*) across 4 regions in the southeastern United States during 2020-2021, allowing the interaction of flock type and region.

	Sum of Squares	df	Mean Square	F	Sig.
Between Regions	1.946	3	0.649	23.590	0.000*
Between Flock Types	0.001	1	0.001	0.038	0.844
Region*Flock Type	0.505	3	0.1683	6.119	0.000*
Residuals	28.439	1034	0.0275		

* $P < 0.001$

Table 2.2: Average distance (dist) in kilometers between relatives within order and region with associated standard error (se) and total number of dyads (*n*) for eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2020-2021.

Region	Order	dist	*n*	se
Piedmont	1st-Order	3.93	32	1.39
Piedmont	2nd-Order	2.80	27	1.35
Piedmont	3rd-Order	4.91	39	1.22
Piedmont	Unrelated	14.69	2248	0.23
SELA	1st-Order	0.74	118	0.40
SELA	2nd-Order	3.02	98	0.60
SELA	3rd-Order	6.04	198	0.44
SELA	Unrelated	17.35	5364	0.13
SRS	1st-Order	3.03	19	1.30
SRS	2nd-Order	7.88	12	2.23
SRS	3rd-Order	10.84	32	1.30
SRS	Unrelated	11.54	3592	0.11
WLA	1st-Order	2.42	39	0.85
WLA	2nd-Order	5.31	34	1.25
WLA	3rd-Order	7.76	113	0.81
WLA	Unrelated	32.01	3384	0.36

Table 2.3: Distance summaries (average Euclidean distance in km) of same-sex (male-male and female-female) and mixed-sex (male-female) dyads of adult eastern wild turkeys (*Meleagris gallopavo silvestris*) across 4 regions of the southeastern United States during 2020-2021.

Male-Male Dyads

Region	Order	avg	*n*	se
Piedmont	1st	0.00	1	*NA*
Piedmont	3rd	1.33	1	*NA*
SELA	1st	0.47	15	0.41
SELA	2nd	4.27	6	1.36
SELA	3rd	3.41	10	1.16
SRS	1st	5.48	6	3.62
SRS	2nd	6.66	2	0.00
SRS	3rd	13.48	2	9.18
WLA	1st	0.01	2	0.01
WLA	2nd	0.01	2	0.01
WLA	3rd	8.56	19	2.81

Female-Female Dyads

Region	Order	avg	*n*	se
Piedmont	1st	1.08	6	1.08
Piedmont	2nd	0.19	5	0.19
Piedmont	3rd	3.58	11	2.87
SELA	1st	1.87	15	1.27
SELA	2nd	7.06	2	7.06
SELA	3rd	7.34	27	1.34
SRS	1st	1.62	5	1.11
SRS	3rd	14.44	6	3.33
WLA	1st	1.92	15	1.37
WLA	2nd	5.66	11	2.66
WLA	3rd	7.36	46	1.21

Male-Female Dyads

Region	Order	avg	*n*	se
Piedmont	1st	25.23	2	3.43
Piedmont	3rd	13.79	5	3.75
SELA	1st	0.28	7	0.18
SELA	2nd	3.95	9	1.26
SELA	3rd	6.46	33	1.19
SRS	1st	7.99	1	*NA*
SRS	2nd	3.60	2	3.60
SRS	3rd	11.18	11	1.69
WLA	1st	5.12	12	2.00
WLA	2nd	6.91	11	2.10
WLA	3rd	11.07	22	1.66

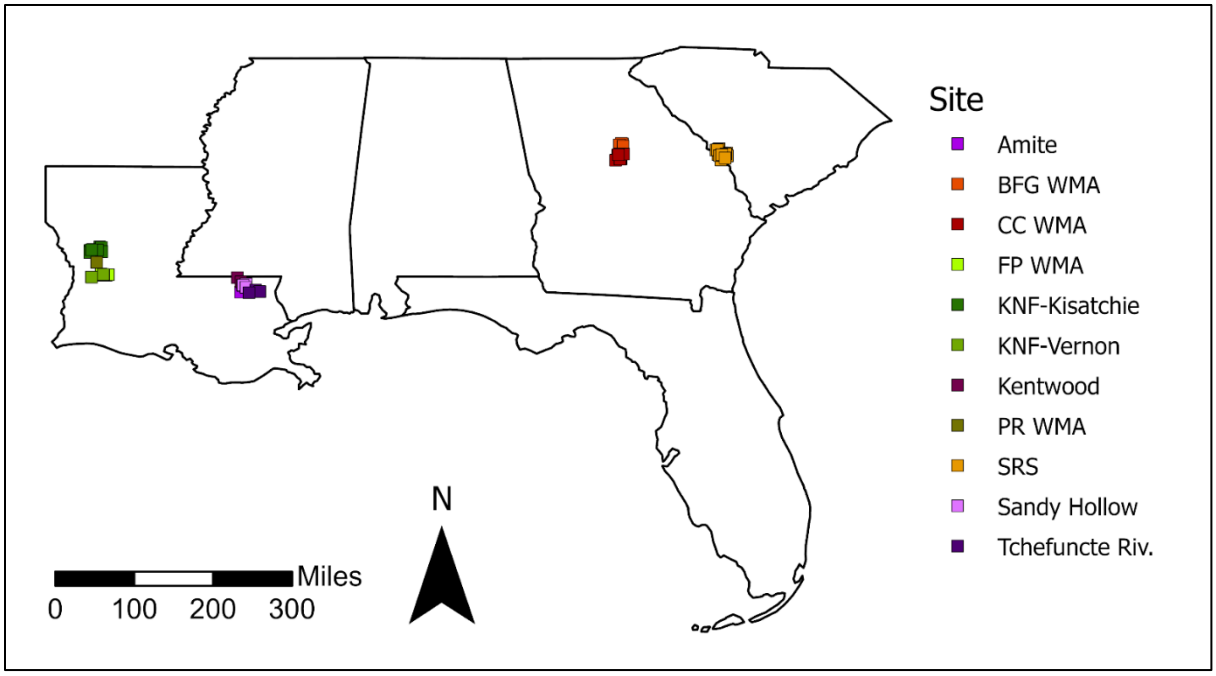


Figure 2.1: Location of sampling site across 4 regions of the southeastern United States. The legend is ordered alphabetically with sites within the same region sharing color schemes (WLA = *green*, SELA = *purple*, Piedmont = *red*, SRS = *orange*).

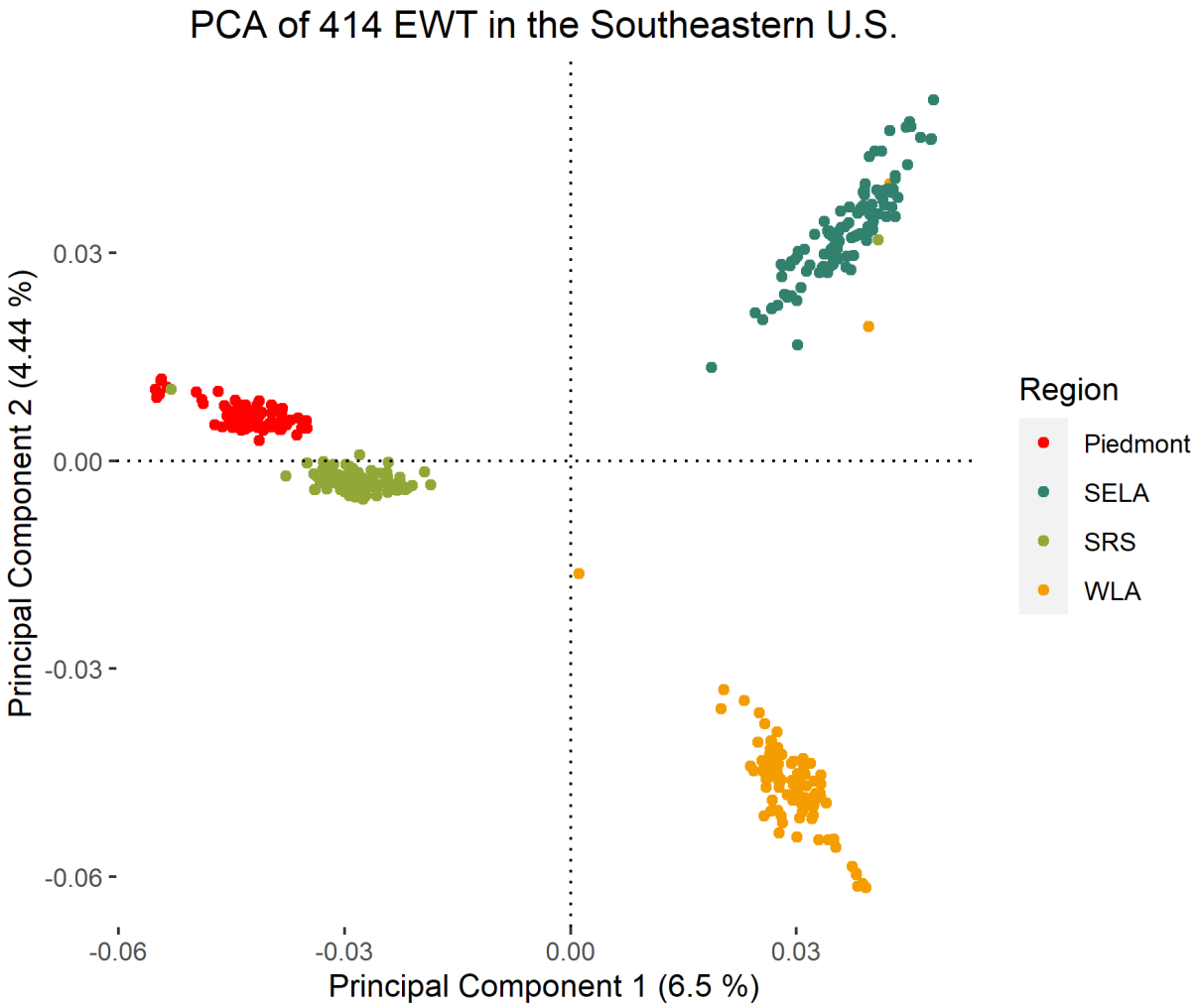


Figure 2.2: A principal component analysis of eastern wild turkey (EWT; *Meleagris gallopavo silvestris*) population genomic structure showing clustering occurring across 4 regions in the southeastern United States from 2020-2021. Variation explained by each principal component is shown on the corresponding axis. Regional designations, which included the Piedmont of Georgia (Piedmont), southeastern Louisiana (SELA), Savannah River Site (SRS), and western Louisiana (WLA) reflect *a priori* assignments based on trap location.

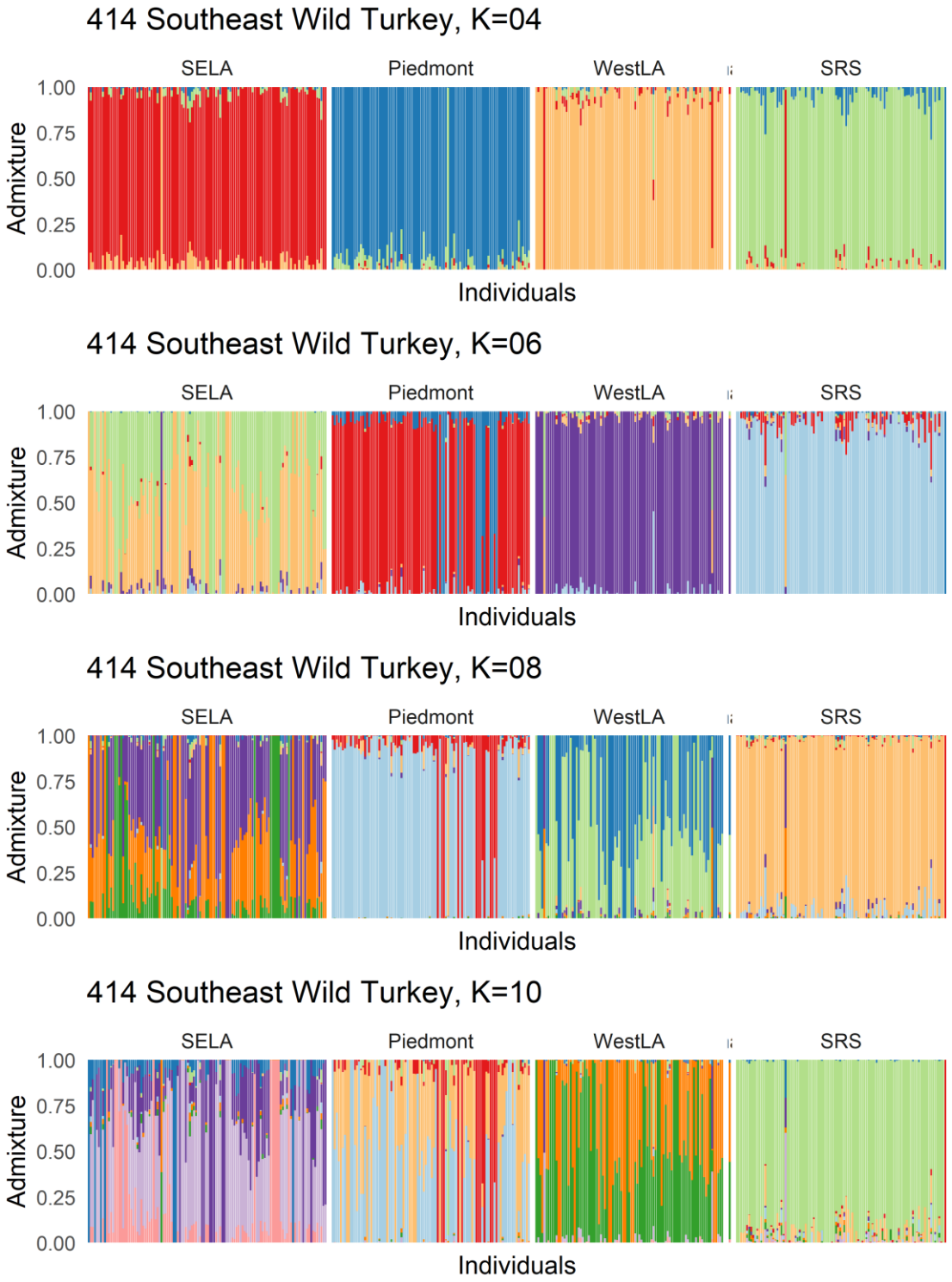


Figure 2.3: Individual cluster (*K*) assignment probabilities from *ADMIXTURE* results of 414 eastern wild turkeys (EWT; *Meleagris gallopavo silvestris*) from 2020-2021. Individuals are represented on the x-axis by narrow vertical bars and are faceted by *a priori* regional

assignments. Regional assignments include southeastern Louisiana (SELA), the Piedmont of Georgia (Piedmont), western Louisiana (WLA), and Savannah River Site (SRS). The y-axis represents each turkey's estimated proportion of membership to each cluster.

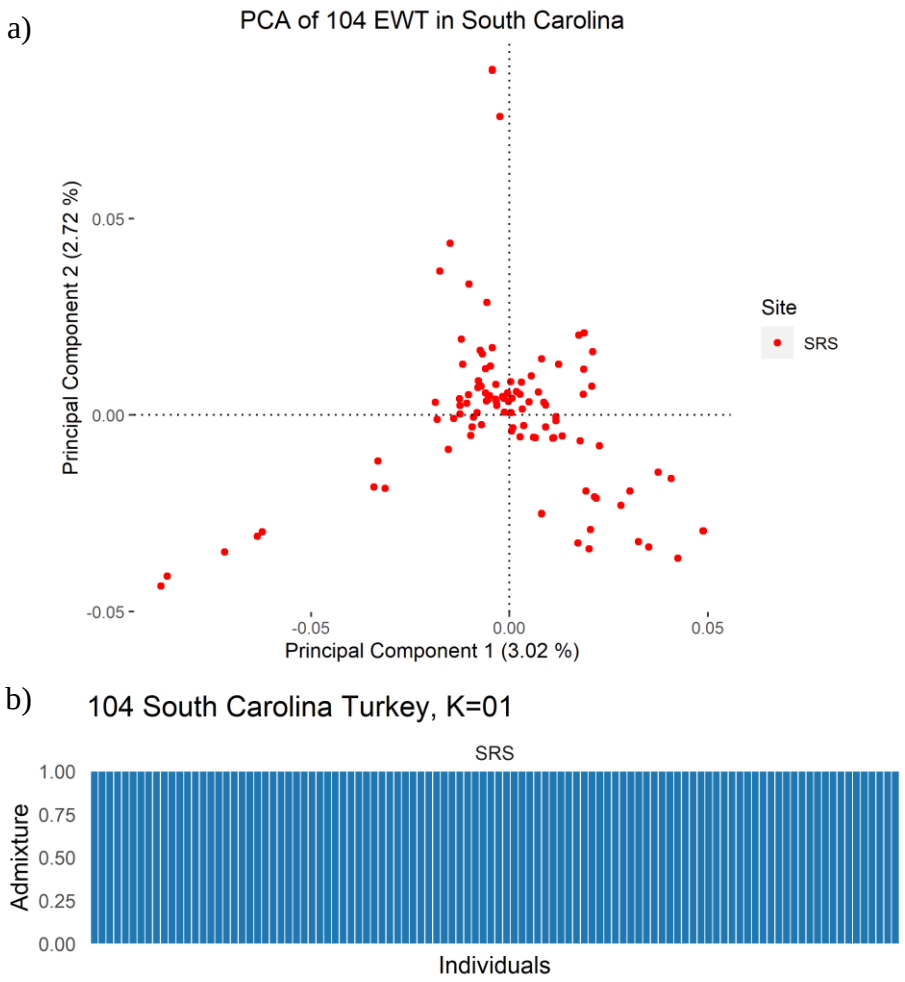


Figure 2.4: a) Genetic structure inferred by a principal component analysis of 104 eastern wild turkey (EWT; *Meleagris gallopavo silvestris*) at the Savannah River Site, South Carolina, USA 2020-2021 (SRS) showing no clustering within the population. Variation explained by each principal component displayed on the corresponding axis. B) Individual assignment probabilities from *ADMIXTURE* results are displayed in a bar graph. Individuals are represented by vertical bars along the x-axis. Cross-validation suggested samples belong to a single population (*K*=1) indicating no population substructure exists at SRS.

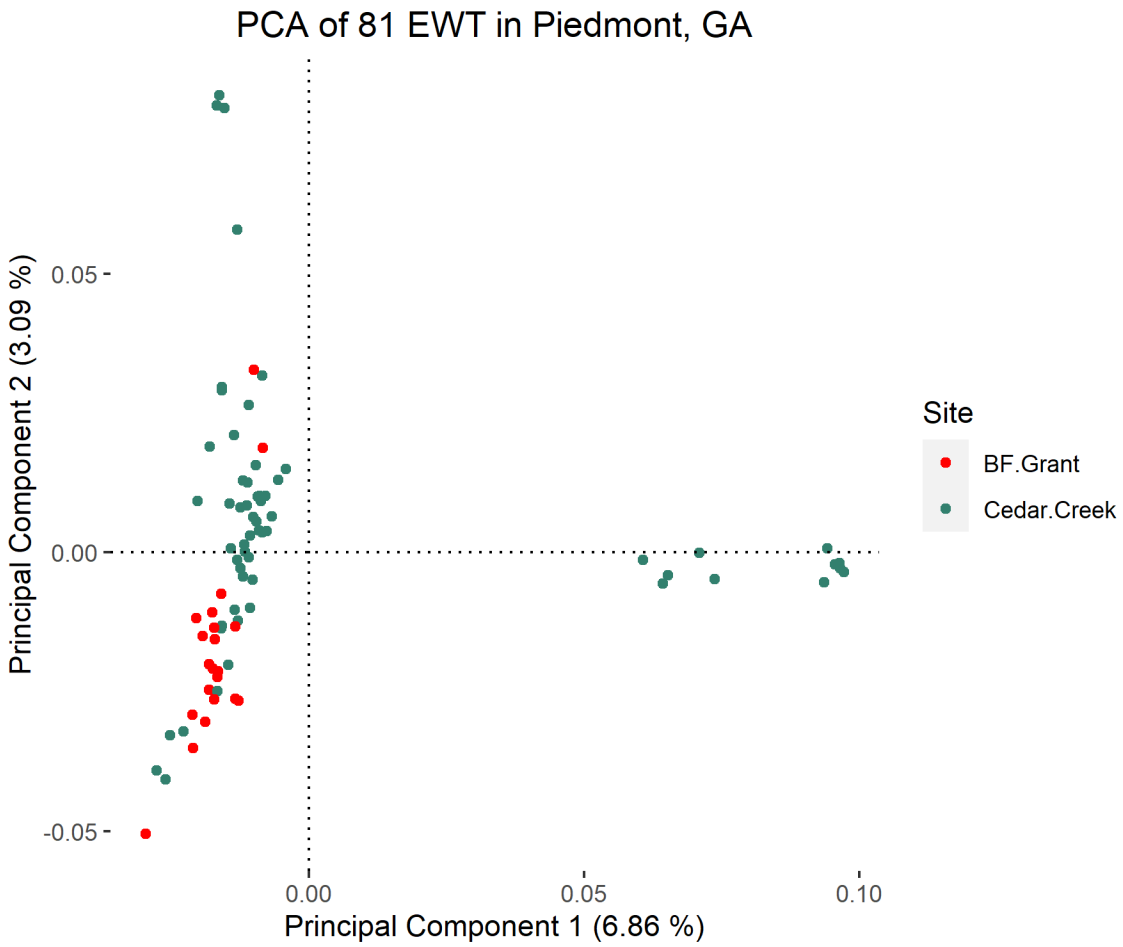


Figure 2.5: Genetic structure inferred by a principal component analysis of 81 eastern wild turkey (*Meleagris gallopavo silvestris*) in Piedmont, Georgia, USA 2020-2021 (Piedmont) showing two population clusters. Site designations correspond to *a priori* assignments based on trap locations. Variation explained by each principal component displayed on the corresponding axis.

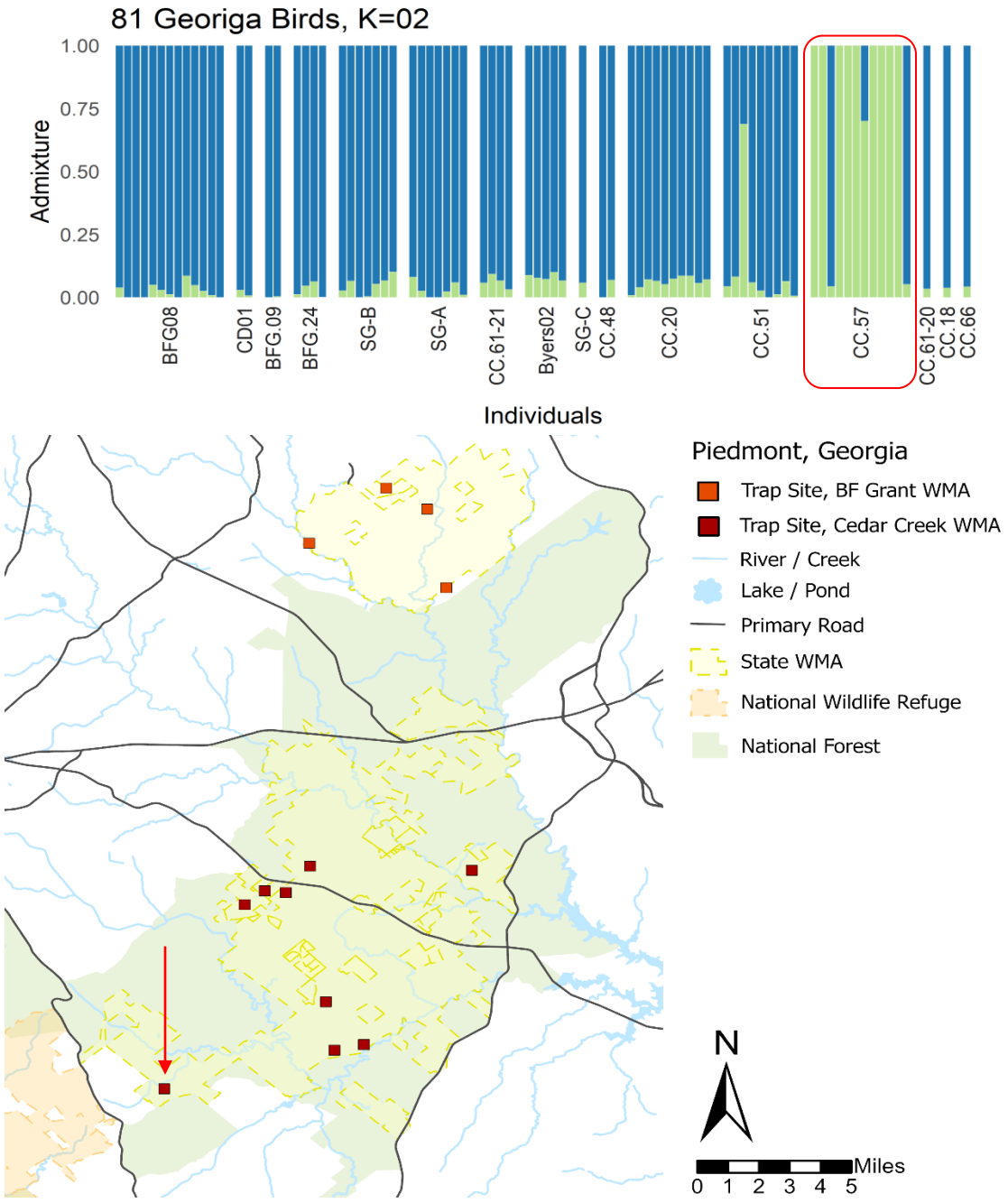


Figure 2.6: a) Individual assignment probabilities represented in a vertical bar graph from *ADMIXTURE* analysis of 81 eastern wild turkeys (*Meleagris gallopavo silvestris*) in Piedmont, Georgia, USA 2020-2021 (Piedmont). Individuals are faceted on the x-axis by *a priori* winter flock assignments. B) Locations of trap sites for the Piedmont, Georgia. The red arrow highlights the trap location of flock CC 57.

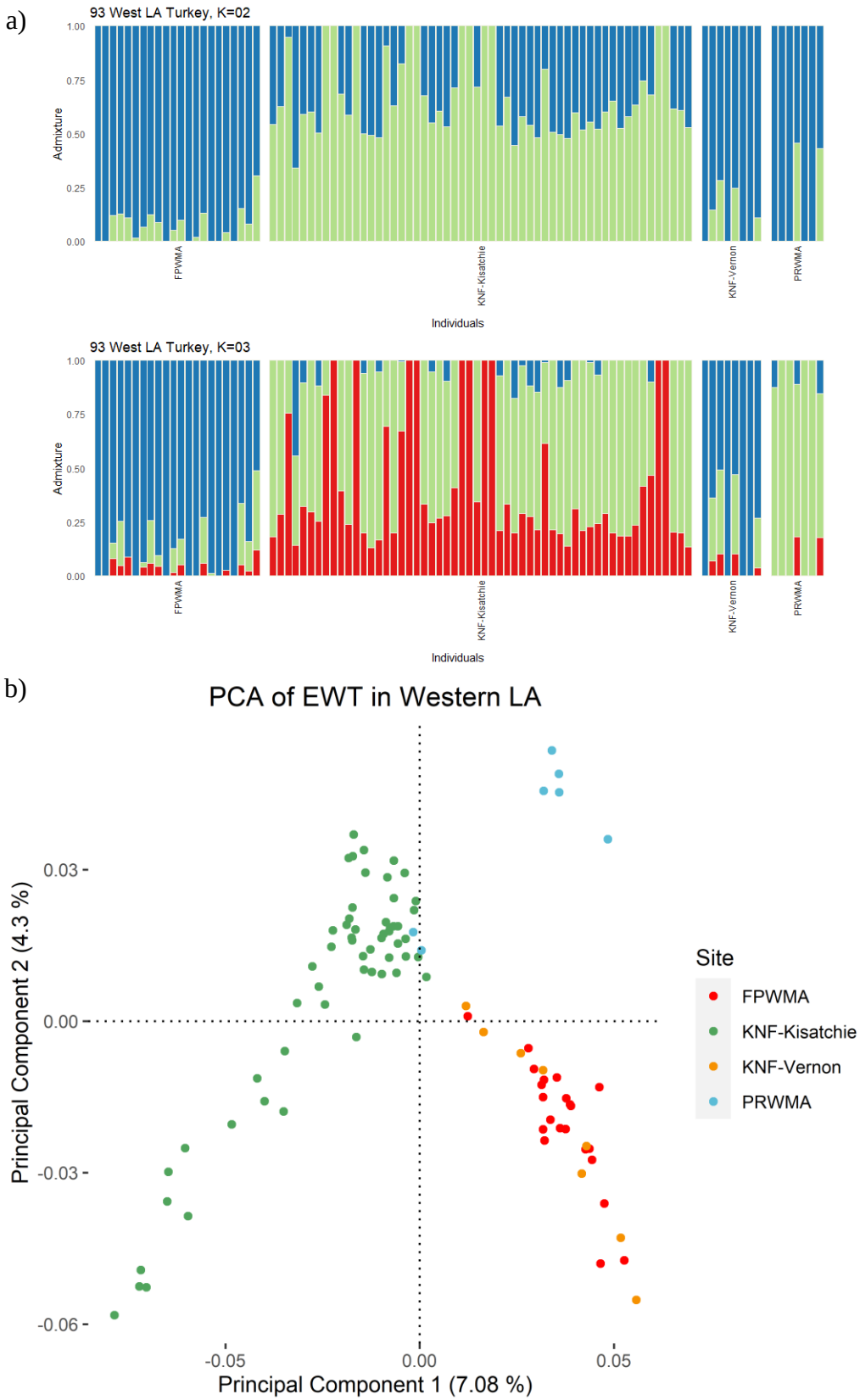
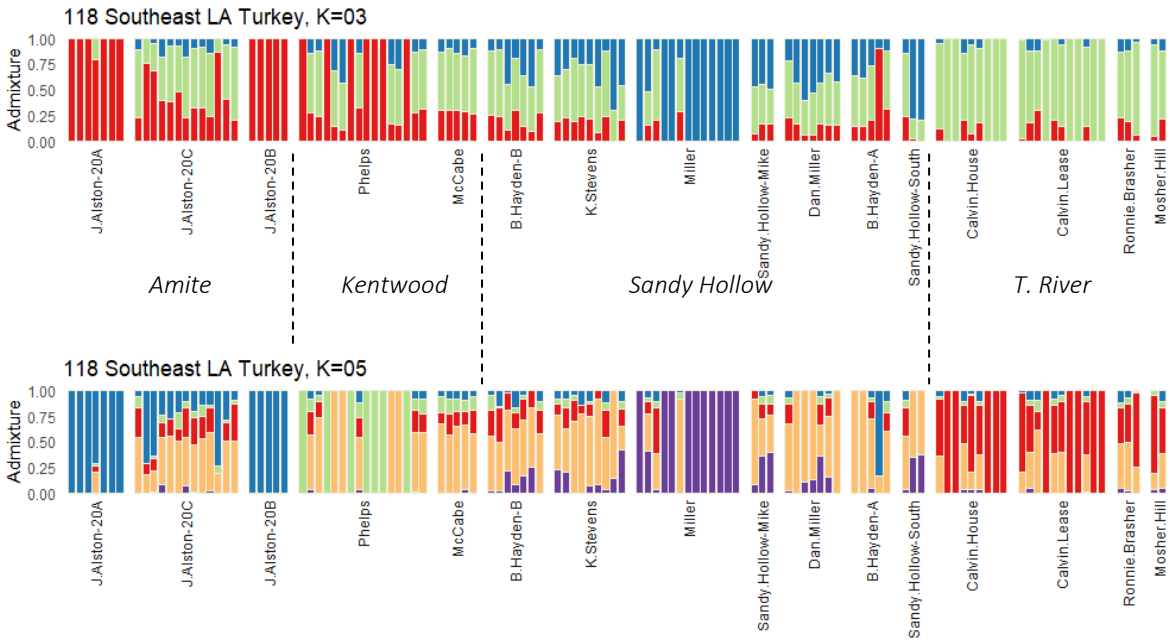


Figure 2.7: a) Individual assignment probabilities represented in a vertical bar graph from

ADMIXTURE analysis of 93 eastern wild turkey (EWT; *Meleagris gallopavo silvestris*) in western Louisiana, USA 2020-2021 (WLA). Results are faceted by *a priori* site designations which included Fort Polk WMA (FPWMA), Kisatchie National Forest-Kisatchie Unit (KNF-Kisatchie), Kisatchie National Forest-Vernon Unit (KNF-Vernon), and Peason Ridge WMA (PRWMA). Cross-validation optimized at K=2. B) Genetic structured inferred by a principal component analysis of 93 EWT in WLA reveals site level clustering. Site designations correspond to *a priori* assignments based on trap locations. Variation explained by each principal component displayed on the corresponding axis.

a)



b)

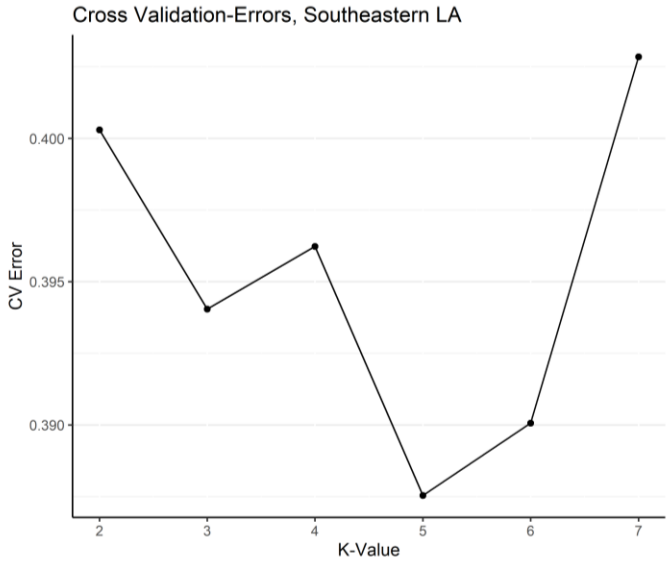


Figure 2.8: a) Individual assignment probabilities for 118 eastern wild turkeys (*Meleagris gallopavo silvestris*) in southeastern Louisiana, USA (SELA; 2020-2021). Individuals are faceted along the x-axis by *a priori* flock designations and are ordered alphabetically by *a priori* site designations. B) Graph of *ADMIXTURE* cross-validation errors for each assessed *K*-value in southeastern Louisiana (SELA).

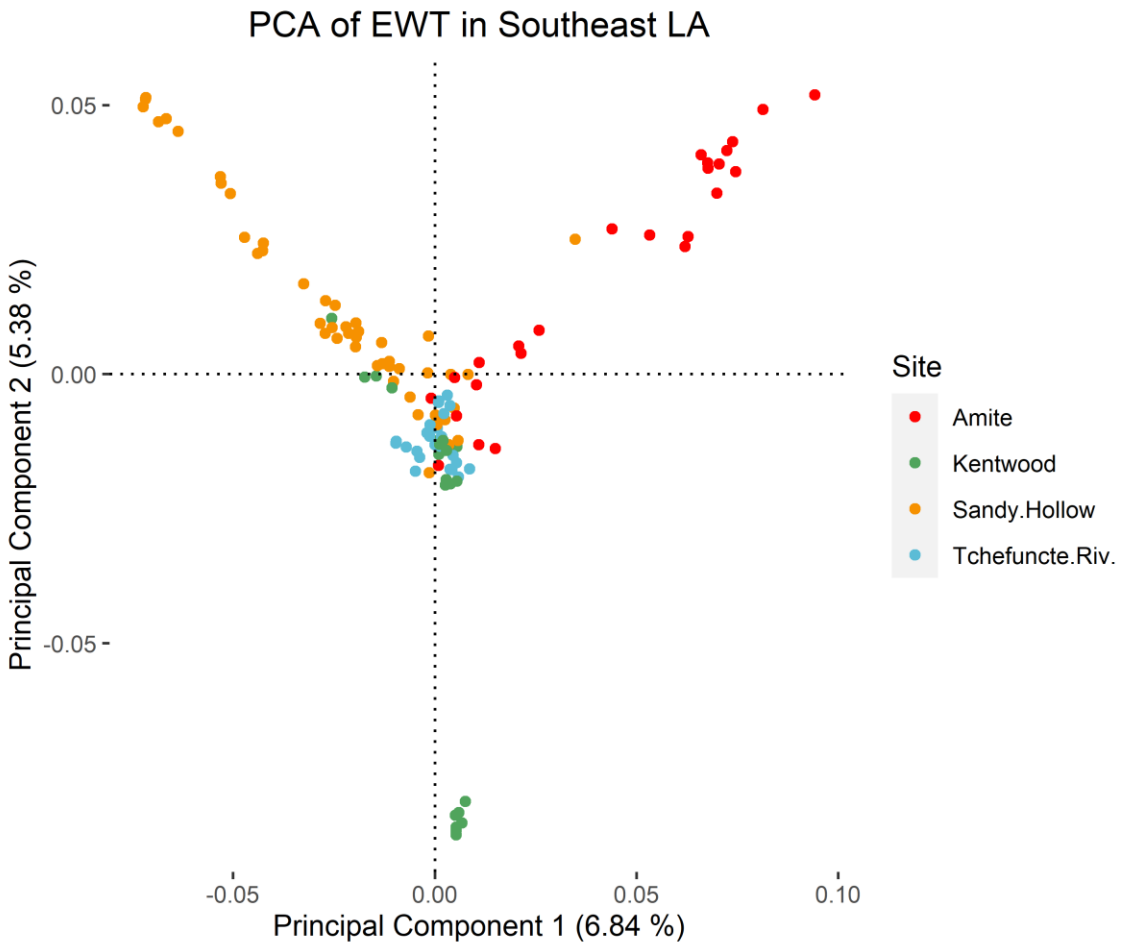


Figure 2.9: Genetic structured inferred by a principal component analysis of 118 eastern wild turkeys (EWT; *Meleagris gallopavo silvestris*) in southeastern Louisiana (SELA; 2020-2021). Site designations correspond to *a priori* assignments based on trap locations which included Amite, Kentwood, Sandy Hollow, and Tchefuncte River. Variation explained by each principal component displayed on the corresponding axis.

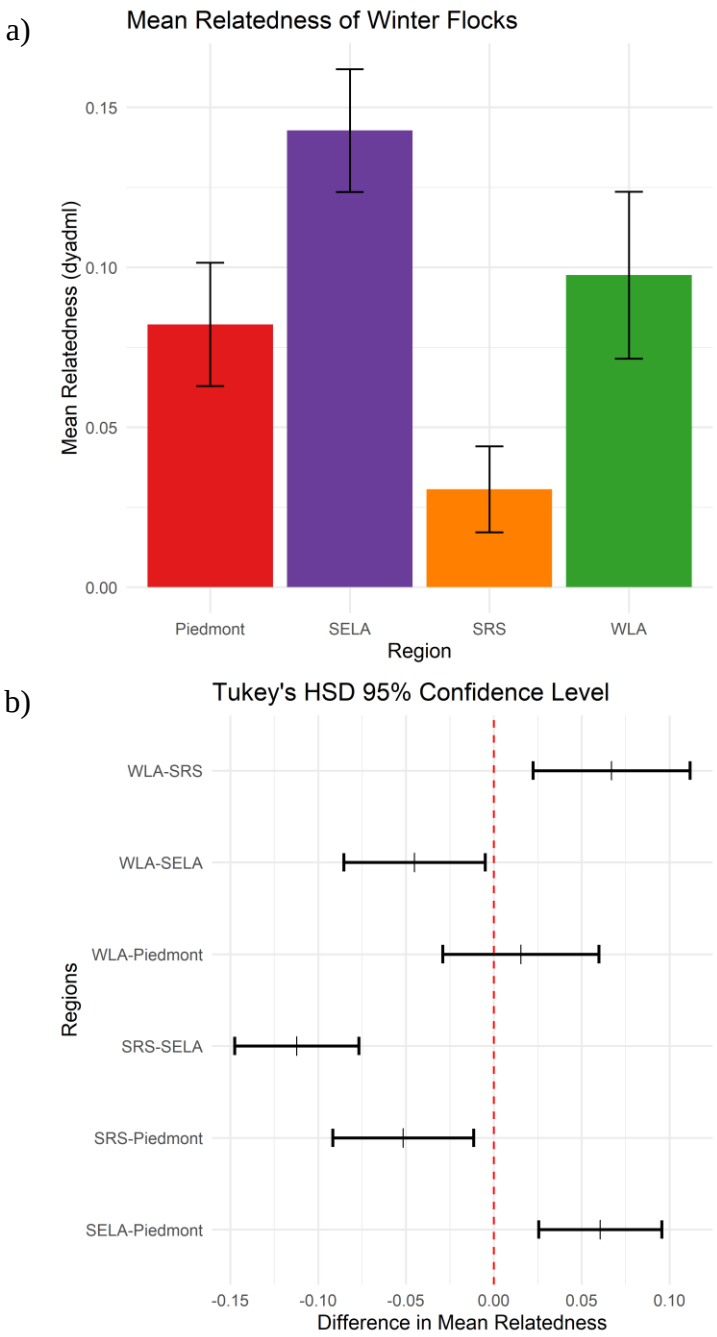
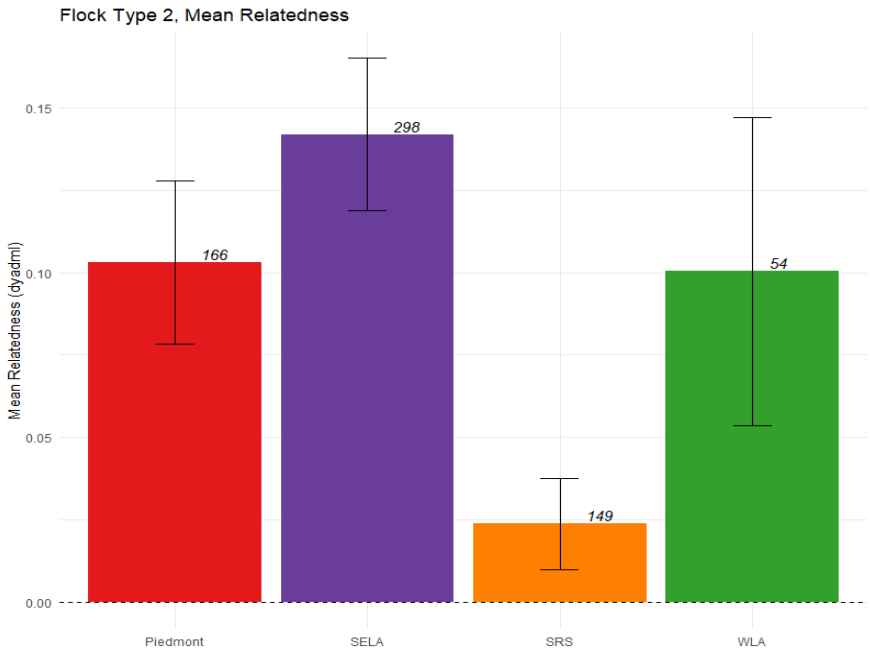


Figure 2.10: a) Mean (± 95% *CI*) coefficients of relatedness I within winter flocks of eastern wild turkey (*Meleagris gallopavo silvestris*) across four regions in the southeastern United States during 2020-2021, and b) a Tukey's HSD test of all pairwise differences in mean relatedness I within winter flocks, among regions. Regions included Piedmont Georgia (Piedmont), southeast Louisiana (SELA), Savannah River Site (SRS), and west Louisiana (WLA).

a)



b)

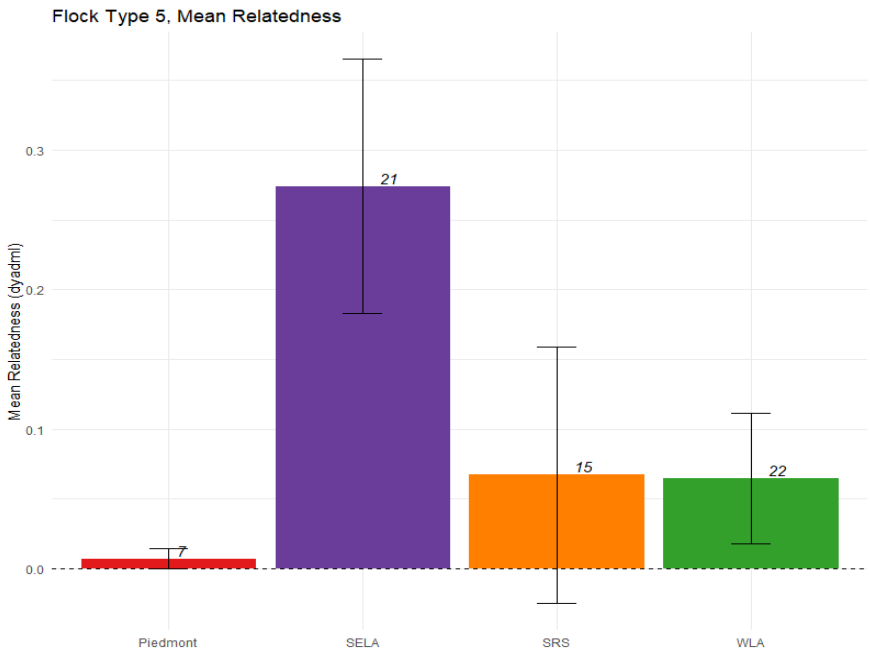


Figure 2.11: a) Mean (± 95% *CI*) coefficients of relatedness I within flocks of adult females with mixed-sex juveniles (flock type 2) by region, and b) mean (± 95% *CI*) coefficients of relatedness

coefficient I within flocks of adult males (flock type 5) by region for eastern wild turkeys (*Meleagris gallopavo silvestris*) across the southeastern United States during 2020-2021. Regions include the Piedmont Georgia (Piedmont), southeast Louisiana (SELA), the Savannah River Site (SRS) and western Louisiana (WLA).

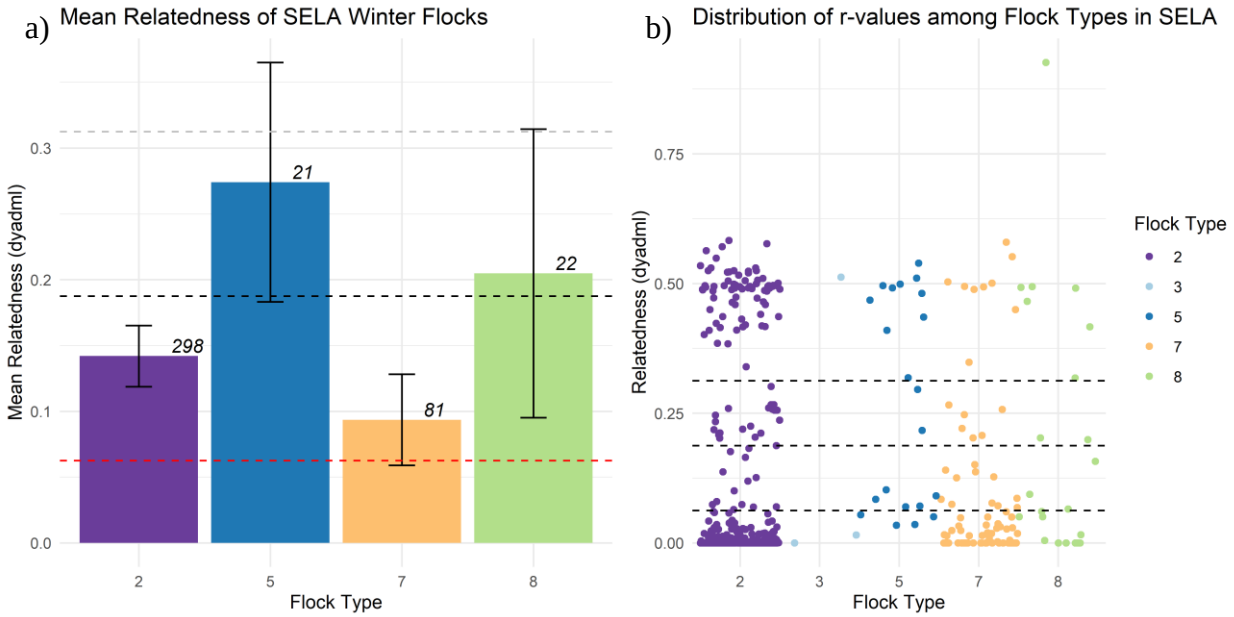


Figure 2.12: Averages and distribution of coefficients of relatedness I of eastern wild turkey (EWT; *Meleagris gallopavo silvestris*) for each flock type within southeast Louisiana (SELA) from 2020-2021. Flocks are binned into categories based on their sex and age composition: [2] adult females with mixed-sex juveniles, [3] mixed-sex juveniles, [5] adult males, [7] mixed-sex adults and juveniles, and [8] mixed-age males. A) Mean (± 95% *CI*) coefficients of relatedness I for each flock type within SELA, where dashed horizontal lines indicate relatedness bin thresholds. Thresholds from bottom-to-top are as follows, unrelated (UR, $r < 0.0625$, 3rd-order ($r \geq 0.0625$ & < 0.1875), and 2nd-order ($r \geq 0.1875$ & < 0.3125). b) Distribution of relatedness coefficients I within each flock type in SELA. Dashed-horizontal lines indicate relatedness bin thresholds. Thresholds from bottom-to-top are as follows, 3rd-order ($r \geq 0.0625$ & < 0.1875), 2nd-order ($r \geq 0.1875$ & < 0.3125), and 1st-order ($r > 0.3125$).

Figure 2.13: Distribution of distances (km) between relatives of the 1st (a), 2nd (b), and 3rd (c) order of eastern wild turkeys (*Meleagris gallopavo silvestris*) across 4 regions in the southeastern United States during 2020-2021. Points are vertically jittered +/-0.5 around the y-axis to unstack points and show data trends.

CHAPTER 3

THE ROLE OF KINSHIP IN SOCIALITY OF FEMALE EASTERN WILD TURKEYS (*MELEAGRIS GALLOPAVO SILVESTRIS*)[2]

[2] Watkins, S.W., B. M. vonHoldt, J. A. Martin, and M.J. Chamberlain. To be submitted to *The Auk: Ornithological Applications*.

Abstract

Quantitative analysis of dynamic social interactions and the influence of kinship on social group membership can provide improved understanding of animal behavior well beyond the limits of what is feasible through traditional static indices. Miniaturization and technical improvements of remote tracking devices have alleviated historic barriers to studying social connectivity. Female wild turkeys (*Meleagris gallopavo*) exhibit seasonal variation in gregarious behaviors, making them a candidate species for investigating social networks in wild systems. We used a matrix of contact rates generated from high-resolution GPS data of 155 female wild turkeys across 4 regions in the southeast US to quantify dynamic interactions and visualize social networks. We noted that social networks underlying female movements and group dynamics were complex and variable. By plotting contact rates for each social group temporally, we were able to monitor how groups dissolved as they transitioned from winter flocks to pre-laying harems, and subsequently into laying/incubating ranges. Sixty-seven percent (n = 22,212) of all contacts occurred when females were in the pre-laying phase, 29% (n = 9,793) were between females who did not attempt a nest, and 2.9% (n=956) occurred during the laying phase. Using 3,789 SNP variants per female to calculate genetic relatedness of individuals within and among social groups, we determined that 94% of all social contacts occurred between unrelated individuals. Additionally, we noted that 60% of females who had a genetic relative in their winter flock did not join a social group, suggesting females identify a cost to association with kin during the reproductive season.

Introduction

Understanding animal movements is critical to describing basic species biology and is an increasingly important topic for conservation of species that are spatially structured. Animals move to locate and exploit resources while avoiding risk, as such movements have been shaped over broad temporal periods through ecological processes and evolution (Nathan 2008). Direct observation of species is difficult and close proximity between observer and animal can cause significant influences in movement behavior (Scharf et al. 2016). Electronic tags were engineered to curb observer effects on animal behavior and have been used in animal tracking since the 1960s (Lord et al. 1962). Traditional tags and other remote tracking tags using very-high frequency (VHF) have revealed general patterns of animal space use, but data suffers from biases associated with distance between observer and transmitter as well as animal movement between readings (Kays et al. 2015, Cohen et al. 2018). Recent miniaturization and technical improvements of global positioning system (GPS) tracking devices allows collection of high-resolution, multi-individual movement data and can document dynamic interactions of individuals (Millspaugh et al. 2004, Kays et al. 2015). High-temporal resolution data can document brief interactions between animals, giving researchers opportunities to study social networks and dynamic movement/interactions between multiple individuals (Kays et al. 2015).

Conspecifics may maintain overlapping home ranges, where several individuals use the same characteristics of their habitat with or without direct interactions (Brown and Orians 1970, Börger et al. 2008, Rutschmann et al. 2020). Interactions can be characterized as static or dynamic (Macdonald et al. 1980), with static interactions being those that define the joint-space use of 2 individuals and reveal the extent of home range overlap, but not how conspecifics influence each other's movements (Kernohan et al. 2001). Dynamic interactions consider

whether 2 animals use the same space simultaneously or at different times (Macdonald et al. 1980, Doncaster 1990, Millspaugh et al. 2004, Alba-Mejia et al. 2013), and imply a degree of static interaction, whereas the converse is not necessarily true (Long et al. 2014). Social networks underly moving object clusters such as bird flocks, and can help explain conspecific interactions and a myriad of other behavioral activities (Li et al. 2013, Scharf et al. 2016). Social networks are commonly defined based on directly measurable behaviors, such as the duration of time animals spend in close proximity or discrete counts of interactions (Scharf et al. 2016). Likewise, social networks may be shaped by dominance hierarchies and have potential to influence many aspects of avian life history (Noble 1939). Wild turkeys (*Meleagris gallopavo*) exhibit seasonal variation in gregarious behaviors, and are known to have pronounced dominance hierarchies, making them a candidate species for investigating social networks in wild systems.

Contemporary research on sociality in wild turkeys has focused primarily on males, seeking evidence of kin selection to describe the mating system and understand how hunter harvest of males during the reproductive period could influence population ecology (Krakauer 2005;2008, Lott 2022). However, much of this research was based solely on visual observations or static home range indices (Krakauer 2005;2008). Female wild turkeys are known to exhibit seasonal variations in social behavior, with more gregarious behaviors being common in winter (Watts and Stokes 1971, Healy 1992). However, the onset of reproduction changes female tolerance of conspecifics, the timing of which is primarily controlled by photoperiod, although local weather, disturbance, and social hierarchies can also influence the timing and distribution of reproductively-active females (Robel and Ballard 1974, Foster 1983, Healy and Nenno 1985, Vangilder et al. 1987). As spring approaches and day-length increases, females dissolve winter

flocks and form smaller social groups associated with a group of males that may, or may not, be related (Watts and Stokes 1971, Krakauer 2005;2008), suggestive of an exploded lek mating system (Emlen and Oring 1977, Kotrschal and Taborsky 2010). Hence, females are not distributed uniformly across the landscape during this period, instead clustering into harems of 2-5 with facilitated access to displaying males (Watts and Stokes 1971, Healy 1992, Schrocder and White 1993, Westcott 1997). Based exclusively on visual observations, there appears to be a complete shuffling of female flocks, so sibling females seldom end up in the same harem (Watts 1969, Watts and Stokes 1971). Movement and range size of females between leks are highly variable (Conley et al. 2016, Bakner et al. 2019, Chamberlain et al. 2020) and drive the spatial genetic structure of populations (Coulon et al. 2008, Cushman and Lewis 2010, Alba-Mejia et al. 2013).

With the onset of laying and incubation, female wild turkeys dissolve social groups and begin exhibiting secretive antisocial behaviors (Healy 1992) influenced by the underlying social structure (Scharf et al. 2016). Notable social hierarchies have been shown to influence timing, distribution, and aggregation of breeding females in a lek-centered system (Robel and Ballard 1974, Foster 1983), and avoidance of conspecifics during laying and incubation is thought to provide defense against predators and nest parasites (Healy 1992, Andersson et al. 2019, Sullivan et al. 2022). Conversely, spatial and temporal clustering of conspecifics during early breeding periods (pre-laying) have positive fitness benefits via information transfer of resource availability, predation risk, and mate availability (Forbes and Kaiser 1994, Danchin et al. 1998). Wild turkeys exhibit notable social hierarchies, wherein high ranking males secure higher proportions of breeding and high ranking females obtain preferential access to mates(Watts and Stokes 1971, Eaton 1992, Healy 1992). Males and females maintain separate hierarchies

established through agnostic interactions within juvenile cohorts (Healy 1992), and rank within hierarchies seldom changes as long as the dominant bird survives (Watts and Stokes 1971).

Quantitative analysis of dynamic social interactions and how kinship influences membership within social groups will provide improved understanding of turkey behavior well beyond the limits of what is feasible through traditional static indices. Therefore, we characterized social relationships of female wild turkeys as winter flocks dissolved into social groups, and then as females left these groups to nest. We used high-resolution GPS data to calculate rates and discrete counts of dynamic interactions among females. We then used a matrix of contact rates to visualize social networks and plot interactions within social groups temporally to investigate how reproductive status and relatedness influenced sociality. Based on historic visual observations detailed in Watts and Stokes (1971) we hypothesized that relatedness would influence the composition of social groups. Specifically, we predicted that related females would leave winter flocks and enter different social groups so as not to be within the same harem.

Study Area

We used data from 4 regions in the Southeastern United States within the states of Georgia, Louisiana, and South Carolina. Specifically, I used data from three sites located within the Piedmont region of Georgia, including B.F. Grant Wildlife Management Area (BFG), Cedar Creek Wildlife Management Area (CCWMA), and Piedmont National Wildlife Refuge (PNWR). Cedar Creek was 15,303 ha located in Jones, Jasper, and Putnam counties. Cedar Creek was owned by the U.S. Forest Service (part of Chattahoochee-Oconee National Forest) and managed in partnership with Georgia Department of Natural Resources – Wildlife Resources Division (GADNR). Landscape composition at Cedar Creek was predominantly upland loblolly pine

stands (Pinus taeda), mixed pine-hardwood forests, and hardwood lowlands dominated by oaks (*Quercus spp.*), sweetgum (*Liquidambar styraciflua*), and hickories (*Carya spp.*). Typical management regimes involved broad-scale prescribed burns during the dormant season on 3–5-year intervals. B.F. Grant WMA was 4,856 hectares located in Morgan and Putnam counties and was owned by the Daniel B. Warnell School of Forestry and Natural Resources at the University of Georgia. In cooperation with the GADNR, prescribed fire was used as the primary vegetation management tool. B.F. Grant consisted of loblolly pine stands, agricultural fields, mixed pine-hardwood forest, and hardwood bottoms of similar composition to Cedar Creek. Piedmont National Wildlife refuge was 14,163 hectares located in Jones and Jasper counties. Landscape composition was predominantly loblolly pine uplands with hardwoods found along riparian areas. Habitat management was focused on needs of the federally endangered red-cockaded woodpecker (*Dryobates borealis*) and included prescribed fire and thinning. For a detailed description of site condition on BFG and CCWMA, see Wakefield et al. (2020).

We used data from 2 sites in western Louisiana (WLA), including Kisatchie National Forest (KNF) and Fort Polk Wildlife Management Area (FPWMA). The KNF was owned and managed by the United States Forest Service (USFS) and FPWMA was jointly owned by the USFS and the United States Army. Both sites were composed of pine (*Pinus spp.*)-dominated forests, hardwood riparian zones, and forested wetlands, with forest openings, utility rights-of-way, and forest roads distributed throughout. Primary overstory species included longleaf pine (*Pinus palustris*), loblolly pine, oaks, hickories, and red maple (*Acer rubrum*). For a detailed description of site conditions on KNFs and FPWMA, see Yeldell et al. (2017a, 2017b).

We used data from a broad suite (~ 2900 ha) of private and public lands in southeastern Louisiana (SELA), including Sandy Hollow WMA (1880 ha) in Tangipahoa and Washington

Parishes. The region was composed of rolling hills with hardwood riparian zones interspersed with young longleaf pine plantations. Agricultural production included grazing and row crops were the dominant land use. For a detailed description of Sandy Hollow WMA, see Duguay et al. (2017).

Lastly, we used data from South Carolina collected on the Savannah River Site (SRS). The SRS was a 78,000-ha former nuclear production facility located in Aiken, Barnwell, and Allendale counties and was owned by the United States Department of Energy. Vegetation communities ranged from sandhills in the xeric uplands to bottomland or swamp forests in low-elevation areas that were subjected to periodic flooding. Management activities included timber production and prescribed fire. For detailed description of site conditions on SRS see Wightman et al. (2019).

Methods

General Methodology

In SELA, WLA, and Piedmont, turkeys were captured from January-March 2020-2021. At SRS, turkeys were captured from January-March and December of 2020 and from January-March of 2021. Turkeys were captured with rocket nets, sexed and aged using the presence (adult) or absence (juvenile) of barring on the 9^{th} and 10^{th} primary feathers (Pelham and Dickson 1992), and marked with an aluminum rivet-style leg band (National Band and Tag company, Newport, Kentucky, USA). Select individuals were fitted with a backpack style GPS transmitter that was remotely downloadable, mortality-sensitive, and equipped with VHF capabilities. Each GPS was programmed to record a location every hour during diurnal periods (0500-2000) throughout prenesting, nesting, and brood-rearing periods (March-July), and one roost location was recorded each night (2359, Cohen et al. 2018). For genomic analysis, a blood sample was

collected from the brachial vein of each individual. The blood was immediately transferred to a microcapillary tube and combined with lysis buffer (100mM Tris, 100 mM EDTA, 10 mM NaCl, 2% SDS). The Tris-EDTA buffer stabilized the solution and allowed for room-temperature storage and shipment of samples. Birds were released at the capture site after processing. Capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University of Georgia (Protocol #A2019 01-025-R2 and A2020 06-018-R1) and Louisiana State University (Protocol #A2018-13).

Reduced Representation Sequencing and Data Processing

The DNA was extracted from blood samples at Princeton University using Qiagen Dneasy blood and tissue kits (Qiagen, Maryland, USA) following manufacturer protocols. We sequenced data using a restriction site-associated DNA sequencing (RADseq) method (Ali et al. 2016) and cleaned them using STACKS v2 (Catchen et al. 2013). We determined single-nucleotide polymorphism (SNP) variants for each genome and made a catalog of all variants detected, at which point we genotyped individuals for SNPs in the catalog. We pruned the initial set of loci using PLINK v1.9 (Purcell et al. 2007), then followed a multi-step filtering process. After initially filtering out loci with >10% missing data (--geno 0.1) and calculating the remaining missing data per sample, there was an obvious tail of low-quality samples. Therefore, we removed samples that had >15% missing data (--mind 0.15) and recalculated missing data per loci. Most loci had low missing data, so we removed a small tail of low-quality loci that had >5% missing data (--geno 0.05). This left the data set with 358,094 variants for 414 individuals. For calculating genetic relatedness, we required a statistically unlinked set of SNP loci, hereafter the neutral SNP set. We filtered for linkage disequilibrium (LD) in PLINK using the flag and

parameters –indep-pairwise 50 5 0.5. We then filtered SNPs to retain those in Hardy-Weinberg equilibrium (--hw 0.001) and with minor allele frequencies (MAF) below 0.40 (--maf 0.40).

Relatedness

We calculated the pairwise relatedness of individuals using the coancestry function in the package *related* (Pew et al. 2015). The package provided a suite of relatedness estimators, and to determine the estimator that best suited our dataset, we simulated 100 pairs of individuals for each degree of relatedness. We then calculated correlation coefficients between the observed and expected relatedness values for each estimator and selected the relatedness estimator that resulted in the highest correlation coefficient. Simulations revealed that the dyad maximum likelihood estimator (dyadml) and the Lynch and Ritland estimator (lynchrd) had the highest correlation coefficients in all regions (Lynch and Ritland 1999, Milligan 2003). We selected dyadml because it is constrained so that minimum relatedness is always 0 and pairwise estimates reflect biologically interpretable relationships between individuals (Milligan 2003). We binned relatedness coefficients into 4 categories: unrelated (UR) < 0.0625, 3^{rd}-order ≥ 0.0625 & < 0.1875, 2^{nd}-order ≥ 0.1875 & < 0.3125, and 1^{st}-order ≥ 0.3125 (Table 3.1). First-order relatives typically reflect parent-offspring or full-siblings, whereas half-siblings, grandparents, cases of extra-pair paternity (EPP) by related males, and quasi-parasitism (QP) from a related female typically fall within the second order. Specifically, EPP is the result of copulation between a female and multiple males, whereas QP occurs when a female lays an egg in another female's nest, and that egg is fertilized by a male already represented at the parasitized nest (Griffith et al. 2004). The third order reflected distant relatives including but not limited to cousins, great grandparents, and many combinations of EPP and QP.

Female Monitoring During Reproductive Period

We monitored all females fitted with a GPS transmitter ≥ 5 times weekly during the nesting season. Upon onset of incubation, we monitored females daily without disruption until nest success or failure. We used ArcGIS 10.3.1 to map GPS data and determine initiation of egg laying and onset of incubation. Because females rarely visit their nest sites before laying the first egg, we denoted the first date females visited the nest site as the onset of laying (Conley et al. 2016, Collier et al. 2019). We defined the laying period as the period during which the female made daily trips to the nest site but roosted elsewhere (Collier and Chamberlain 2011, Conley et al. 2016). The first nightly roost location to occur at the nest site defined the onset of nest incubation (Bakner et al. 2019). The incubation period began when roosting was confirmed to occur at the nest site, and subsequent GPS locations clustered within a 50-meter buffer around the nest site (Conley et al. 2015). Locations with positional dilution of precision (DOP) values ≥ 7 reflect GPS errors and were removed from the dataset. Following nest termination, researchers located the nest site and confirmed an attempt was made based on the presence of eggs, eggshell remains, or a shallow ground depression.

Proximity Analysis

A dyad represents the smallest possible social group (a pair of individuals) and is the first step in analyzing collective behavior of social groups (flocks, Joo et al. 2018) . We calculated the daily contact rate for each possible dyad of females within a study site using the conProcess function within the wildlifeDI package (Long et al. 2014) in R (R Core Team 2021). To track changes in social group composition from winter flocks to harems of females that form during the pre-laying period, and then transition into laying/incubation ranges, we selected a date range from March 15th to April 15th (hereafter days 1-32). We denoted April 15th as the average peak

incubation for wild turkeys in the southeastern US, based on dates reported in several recent works (Little et al. 2014, Crawford et al. 2021). For each day, we calculated the contact rate of each dyad as the number of spatially proximate (< 30m) and temporally simultaneous (< 7min) GPS fixes divided by the number of temporally simultaneous fixes (Long and Nelson 2013). Proximity rates approaching 1 indicated individuals spent 100% of their day in close proximity whereas proximity rates approaching 0 indicated the 2 individuals were rarely in close proximity. We considered a continuous contact (or phase) to occur when 2 or more consecutive locations were spatially and temporally proximate. We excluded nightly roost fixes from the analysis, as we were only interested in social behavior during periods of activity. For each day, we classified the female's breeding status as pre-nesting (P), laying (L), incubating (I), failed (F), or did not exhibit laying or incubation behavior during the reproductive season (D).

We used the conMatrix function in the wildlifeDI package to calculate the underlying social network within each region (Long et al. 2014). To visualize social networks, we used the iGraph package (Csárdi and Nepusz 2006) in R (R Core Team 2021). We distinguished 2 types of social groups, linear and non-linear. In non-linear social groups, every female interacted with all group members. Conversely, in linear social groups not all females interacted with each other, and interactions were typically initiated by a single female. We used package ggplot2 to visually examine daily proximity rates within each social group in relation to each dyad's relatedness category, and we used the daily contact rates to map contact densities as a progression through time (Wickham 2016).

Results

We captured 85 and 156 females during 2020 and 2021, respectively. We excluded 23 females captured in 2020 from analysis due to mortality or transmitter failures, and an additional

5 during the SNP filtering process. We excluded 51 females captured in 2021 from analysis due to mortality or transmitter failures, and an additional 7 during the SNP filtering process. The final data set included GPS data of 155 females and 3,789 SNP variants per female across 2 years and 4 study regions.

Using the matrix of contact rates, we formed weighted social networks and identified 31 social groups (21 non-linear social groups and 10 linear). Non-linear social groups ranged from 3-9 individuals, and typically contained at most one juvenile member, although some larger groups (5-9 individuals) contained a second juvenile. Linear social groups ranged from 2-4 individuals, and typically contacts were initiated by a single female and were non-continuous. The longest continuous contact in each region/year ranged from 7.5-18 days and averaged from 14-53 hours. Social groups (linear and non-linear) usually dissolved 14 days prior to average dates of peak nest incubation (Figure 3.1), although in 2020, we observed extended contacts that lasted through the average peak in nest incubation.

Examination of daily contact rates for all dyads within a defined social group revealed complex and variable dynamics within social groups. Some social groups showed high levels of cohesion, with females repeatedly spending ~ 75% of the day in close proximity (≤ 30m) before concurrently departing the social group (Figure 3.2). Conversely, other social groups exhibited substantive variability in daily contact rates and asynchronous departures from the social group (Figure 3.2).

Social group membership was typically driven by winter flock membership. Whereas some birds in winter flocks did not join a social group (14%), 74% joined a social group composed entirely of members from the same winter flock. Of the females that did not join a social group, 60% had a 1st-order relative in their winter flock. Large winter flocks (> 10

individuals) dissolved into multiple social groups. Six of the 31 social groups contained members from different winter flocks, and 67% of these cases occurred at SRS. We recorded 3 instances of a female switching social groups, and 2 of these instances involved a female leaving her initial social group which contained members of the same winter flock and joining a social group of females whom she spent no time with during winter.

Among females that made ≥ 1 contact with another female, 94% were unrelated. We observed that only 3% of all dyads were 1st-order relatives, and 56% of them contained a juvenile female. Specifically, in the Piedmont contact between 1st-order relatives only occurred when at least one female was a juvenile. Mean contact rate for adult dyads was 0.133 and mean contact rate for dyads containing at least one juvenile was 0.156. Dyads of females containing 1st and 2nd order relatives and juveniles typically had ~50% greater seasonal contact rates compared to adult dyads (Table 3.2). Across all regions, we recorded 50 1st-order relatives (Table 3.1); 40% of females with a 1st-order relative had a seasonal contact rate > 0, followed by 46% of 2nd-order (n = 11), and 32% of 3rd-order (n = 31) relatives.

Sixty-seven percent (n = 22,212) of all contacts occurred when females were in the pre-laying phase, whereas 29% (n = 9,793) were between females who did not attempt a nest. The laying phase only accounted for 2.9% (n = 956) of total contacts. We noted 11 instances where a female was within 30 m of another female during incubation, and 46 after a female had failed her nest attempt. All of the instances where females exhibited contact with another female during incubation involved unrelated females. Contacts during pre-laying and laying were dominated by dyads of unrelated females (79.9% and 90.4% respectively) and followed by 1st-order dyads (16.8% and 8.6% respectively).

Discussion

Our current understanding of social behavior in wild turkeys has been limited to visual observations of interactions and static measures of home range overlap (Watts 1969, Watts and Stokes 1971, Macdonald et al. 1980, Healy 1992, Badyaev et al. 1996*a*, Thogmartin 2001, Miller et al. 2005, Cohen et al. 2018). Historic barriers to studying movement behavior and social connectivity were alleviated by miniaturization and technical improvements of remote tracking devices (Millspaugh et al. 2004, Kays et al. 2015, Scharf et al. 2016). We used a matrix of contact rates generated from high-resolution GPS data of 155 female wild turkeys to quantify dynamic interactions and visualize social networks. We noted that social networks underlying female movements and group dynamics were complex and variable. By plotting contact rates for each social group temporally, we were able to monitor how groups dissolved as they transitioned from winter flocks to pre-laying harems, and subsequently into laying/incubating ranges. Using 3,789 SNP variants per female to calculate genetic relatedness of individuals within and among social groups, we determined that 94% of all social contacts occurred between unrelated individuals.

Group living, expressed through formation of flocks in wild turkeys, is a common trait of many species and is believed to offer individuals reduced predation risk and increased foraging efficiency. However, these benefits must outweigh costs that come with close association of conspecifics, including increased competition for resources such as mating opportunities (Clark and Mangel 1986, Krebs and Davies 1997). Like many avian species, wild turkeys are a gregarious bird that undergo a pronounced breakdown in sociality during the breeding season (Healy 1992, Krause and Ruxton 2002, Lima 2009). As winter flocks dissolve into smaller social groups during the reproductive period, individuals incur positive fitness benefits via information

transfer on resource availability, predation risk, and mate availability (Forbes and Kaiser 1994, Danchin et al. 1998). Likewise, when winter flocks dissolve, individual turkeys alter their space use to form smaller social groups, or breeding harems, to focus efforts on reproduction (Badyaev et al. 1996*b*, Thogmartin 2001). We found that individuals in winter flocks in close geographic proximity (~1 km) would end up as members of the same breeding harem, but more often, breeding harems were comprised of members from a single winter flock, with large winter flocks (≥10 individuals) typically dissolving into multiple harems. We note that instances of individuals from multiple winter flocks ultimately becoming members of the same social group was most common at SRS, a site which has not been exposed to hunting activity or removal of males for decades (Moore et al. 2005). Hunting pressure and the subsequent removal of individuals has been shown to alter many aspects of animal behavior including social behaviors, home range size, reproductive tactics, and more (Verdade 1996, Wightman et al. 2019, Wakefield et al. 2020).

The formation of social groups requires individuals within groups to synchronize activities in order for the group to remain spatially intact (Conradt and Roper 2000). Synchronization requires individual members to compromise their own activity budgets to match the behavior of conspecifics, which can influence whether individuals remain in the group, and thus has consequences for group stability and composition (Conradt and Roper 2000, Davidson and Menaker 2003, Michelena et al. 2008, Hauschildt and Gerken 2015). The dissolution of winter flocks may also be constrained by conspecific attraction/avoidance (Stamps 1988, Jacobs 2010), offering a partial explanation for why larger social groups (i.e., larger winter flocks) typically dissolved into multiple social groups prior to reproduction. It is the cost of both synchronization and social constraints that we believe large social units often disintegrate into

smaller subgroups. From an individual perspective, associating with a relatively small subgroup increases the odds of an individual aligning motivations and needs to that of the group, thus balancing the costs/benefits noted above (Jacobs 2010).

Social cohesion may be observed when an aggregation of individuals remains in visual or vocal contact with most other group members consistently (Boinski 2000). Groups with high levels of cohesion require conspecific social attraction and behavioral synchronization (Jacobs 2010), and we noted that cohesion across social groups was highly variable. Likewise, within groups that exhibit varying cohesion, one or multiple group members may leave the group, sometimes for a couple of hours or days, other times permanently. In various species, kinship has been shown to increase social cohesion through indirect fitness benefits obtained through reduced aggression (Gompper et al. 1997, McCowan et al. 2011), or social learning (Kavaliers et al. 2005). Previous authors have noted that barnacle geese (*Branta leucopsis*) were more likely to forage in groups of related individuals (Kurvers et al. 2013), sub-groups of common eiders (*Somateria mollissima*) arriving at breeding colonies were more closely related to each other than the colony average (McKinnon et al. 2006), and kinship significantly increased within-flock cohesion of house sparrows (*Passer domesticus*; Tóth et al. 2009) and greylag geese (*Anser anser*; Frigerio et al. (2001)). We found that in social groups of female wild turkeys, genetic relatedness within social groups did not differ from average relatedness within winter flocks, and we observed no relationships between kinship and cohesion of social groups. We speculate that varying group cohesion stems from individuals choosing their own motivations over the cost of synchronizing their behaviors to the group. The combination of social and environmental factors that govern interactions amongst individuals makes discerning costs and benefits of interactions fundamental to understanding their occurrence (Silk et al. 2014).

We observed that not all members of winter flocks joined a social group, and more specifically, that the inclusion of juveniles into social groups was limited. Social groups that include members of different age class have higher costs associated with synchronizing activities, because the optimal allocation of time can differ between age classes (Gompper 1996, Conradt and Roper 2000). Additionally, we noted that 60% of females who had a 1st-order relative in their winter flock did not join a social group, suggesting females identify a cost to association with kin during the early reproductive season.

We observed a 95% decrease in contacts during the transition from pre-laying to laying, suggesting females avoid association with conspecifics, regardless of kinship, once the onset of laying begins. As the breeding season progresses into the laying and incubation stages, females presumably adopt reproductive strategies dependent on ecological, social and physiological conditions (Wingfield 1984, Davidson and Menaker 2003, Davies and Deviche 2014, Caro et al. 2015). Furthermore, females may be able to switch strategies between successive breeding periods to include not breeding, pure nest parasitism, self-nesting, and self-nesting combined with parasitism (Andersson et al. 2019). Intraspecific brood parasitism (IBP) is an alternative reproductive strategy among females of egg-laying species, wherein a parasitic female lays eggs in a nest of another female of the same species and hosts then assume costs of incubating and raising the joint brood (Tallamy 2005, Lyon and Eadie 2008). Species such as wild turkeys that lay large clutches and have extended laying periods are more likely to take a parasitic reproductive strategy (Andersson et al. 2019, Sullivan et al. 2022).

The prevalence of IBP has been discussed since the 1980s, and has been linked to the potential that kin selection may be involved (Andersson 1984). If host and parasite are related, then IBP could be described as mutualism through kin-selection rather than true nest parasitism

(Andersson 1984). For example, if host and parasite are related, then it could be described a mutualism through kin-selection (Andersson et al. 2019). In fact, kinship promotes IBP (depending on the number of parasitic eggs) by affording the host potential fitness benefits (Andersson 2001). Sullivan et al. (2022) conducted work on eastern and Rio Grande (*M. g. intermedia*) wild turkeys in the southeastern US and found 6% of nests had the potential to be parasitized based on evidence of a female visiting the nest site of a conspecific during the laying phase. The authors hypothesized that the most plausible explanation for a female visiting the nest site of a conspecific was to lay eggs in clutches of related (mutualism) or non-related (parasitism) females (Sullivan et al. 2022). Conversely, alternative hypothesis such as prospecting for future nesting efforts or communal nesting are unlikely for wild turkeys (Chamberlain et al. 2020, Byrne et al. 2022, Sullivan et al. 2022). Furthermore, Krakauer (2008) used genetic markers to conduct maternity analysis of hatched clutches and found that ~22% of nests were parasitized. Females presumed to be parasitic may associate with host females during the laying period (Sullivan et al. 2022), likely because egg-dumping relies on the ability of the parasitic female to monitor host behavior to secure an attempt at parasitizing when the host is absent (Emlen and Wrege 1986, Petrie and Møller 1991). Likewise, females may avoid conspecific interactions during laying because parasitism reduces host fitness when individuals are not related (Andersson 2001, López-Sepulcre and Kokko 2002). We documented that <3% of contacts amongst females occurred during the laying phase, and 90% of those contacts occurred between unrelated females. If contact between females during the laying period indicates an increased chance of IBP, we speculate that most cases of IBP are parasitism rather than mutualism.

Fitness of a breeding female hinges on individual survival, along with survival of the clutch and brood. Predation of the nest or individual is the leading cause of reproductive failure for wild turkey, and females experience an elevated predation risk during reproduction (Miller and Leopold 1992, Cockburn 2006, Conley et al. 2016). Predation risk can influence reproductive strategies adopted by individual females (Bakner et al. 2019, Lohr 2019), and specifically may increase IBP (McRae 1997, Lyon and Eadie 2008, Andersson et al. 2019). Nest predation is high for wild turkeys requiring several breeding attempts for a female to successfully rear young (Ricklefs 1969, Yeldell et al. 2017, Wood et al. 2019, Chamberlain et al. 2020, Crawford et al. 2021). Because the risk of predation varies within an individual's lifetime and within the reproductive year, evolution favors plasticity in regards to how an individual responds to risk (Lima 2009). We monitored the dissolution of female social systems only through the first peak in nest attempts, but recommend that future works use GPS tracking technologies to monitor additional nesting attempts and investigate plasticity in reproductive strategies in response to predation events and other stochastic processes. Additionally, future research could monitor female social groups across multiple reproductive seasons. Although relationships between brain size and sociality have not been found in birds (Byrne and Bates 2007), cognition could play an important role in maintenance of long-term relationships (Street et al. 2017). Interactions with conspecifics can enable individuals to circumvent their own cognitive limitations and give them access to spatially and temporal context-dependent information (Couzin 2009).

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Table 3.1: Pairwise counts of female eastern wild turkeys (*Meleagris gallopavo silvestris*) within each relatedness category across 4 regions of the southeastern United States during 2020-2021.

		Relatedness[a]			
Region	**Year**	**1st-Order[b]**	**2nd-Order[c]**	**3rd-Order[d]**	**Unrelated[e]**
Piedmont	2020	5	0	6	109
	2021	8	0	5	263
SELA	2020	7	5	3	216
	2021	14	3	12	296
SRS	2021	2	0	0	251
WLA	2020	1	1	3	148
	2021	13	2	2	236
Totals		**50**	**11**	**31**	**1519**

[a] Relatedness coefficient (r) categorized based on value
[b] $r \geq 0.3125$
[c] $r \geq 0.1875$ & < 0.3125
[d] $r \geq 0.0625$ & < 0.1875
[e] $r < 0.0625$

Table 3.2: Summary statistics of all contacts including the number of dyads of female eastern wild turkey (n; *Meleagris gallopavo silvestris*), the mean season (day 1-32) contact rate, and the standard deviation (SD) within each relatedness category (Relatedness), region (Region), and age group (Dyad Contains Juvenile). Age was grouped based on the presence (Yes), or absence (No) of a juvenile female within the dyad. Data were collected from 15 March – 15 April during 2020-2021 across 4 regions in the southeastern United States.

Relatedness	Region	Dyad Contains Juvenile	n	Mean Contact Rate	SD
1st-Order	Piedmont	Yes	4	0.216	0.109
	SELA	No	3	0.136	0.160
	SELA	Yes	4	0.186	0.118
	SRS	No	1	0.100	*NA*
	WLA	No	5	0.333	0.180
	WLA	Yes	3	0.487	0.019
2nd-Order	SELA	No	1	0.100	*NA*
	SELA	Yes	2	0.178	0.075
	WLA	No	2	0.192	0.117
3rd-Order	Piedmont	No	1	0.454	*NA*
	Piedmont	Yes	3	0.108	0.117
	SELA	No	2	0.187	0.214
	SELA	Yes	3	0.185	0.087
	WLA	No	1	0.033	*NA*
Unrelated	Piedmont	No	14	0.072	0.056
	Piedmont	Yes	16	0.084	0.079
	SELA	No	49	0.136	0.138
	SELA	Yes	33	0.125	0.121
	SRS	No	22	0.094	0.094
	WLA	No	57	0.135	0.141
	WLA	Yes	6	0.300	0.083

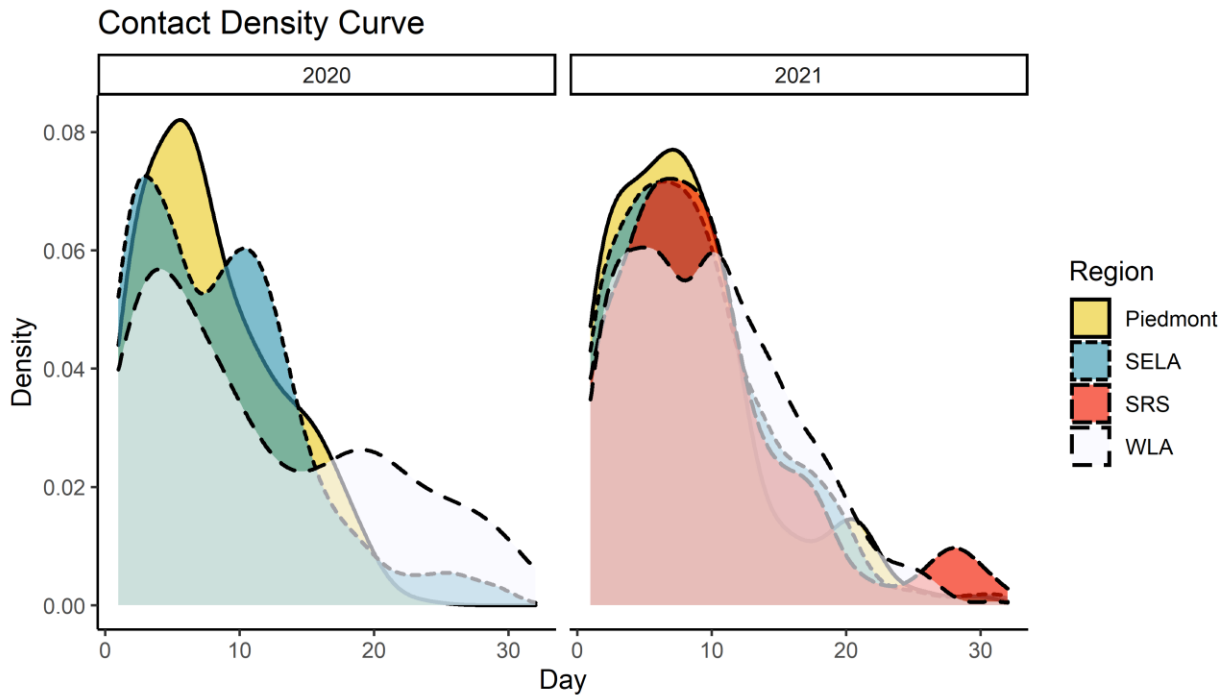

Figure 3.1: Density plot of daily contacts of female eastern wild turkeys (*Meleagris gallopavo silvestris*) from 15 March -15 April during 2020-2021 across 4 regions in the southeastern United States. Date is denoted on the x-axis as number of days from the 15 March (1-32), and density is recorded on the y-axis. Plot was faceted by year and grouped by region.

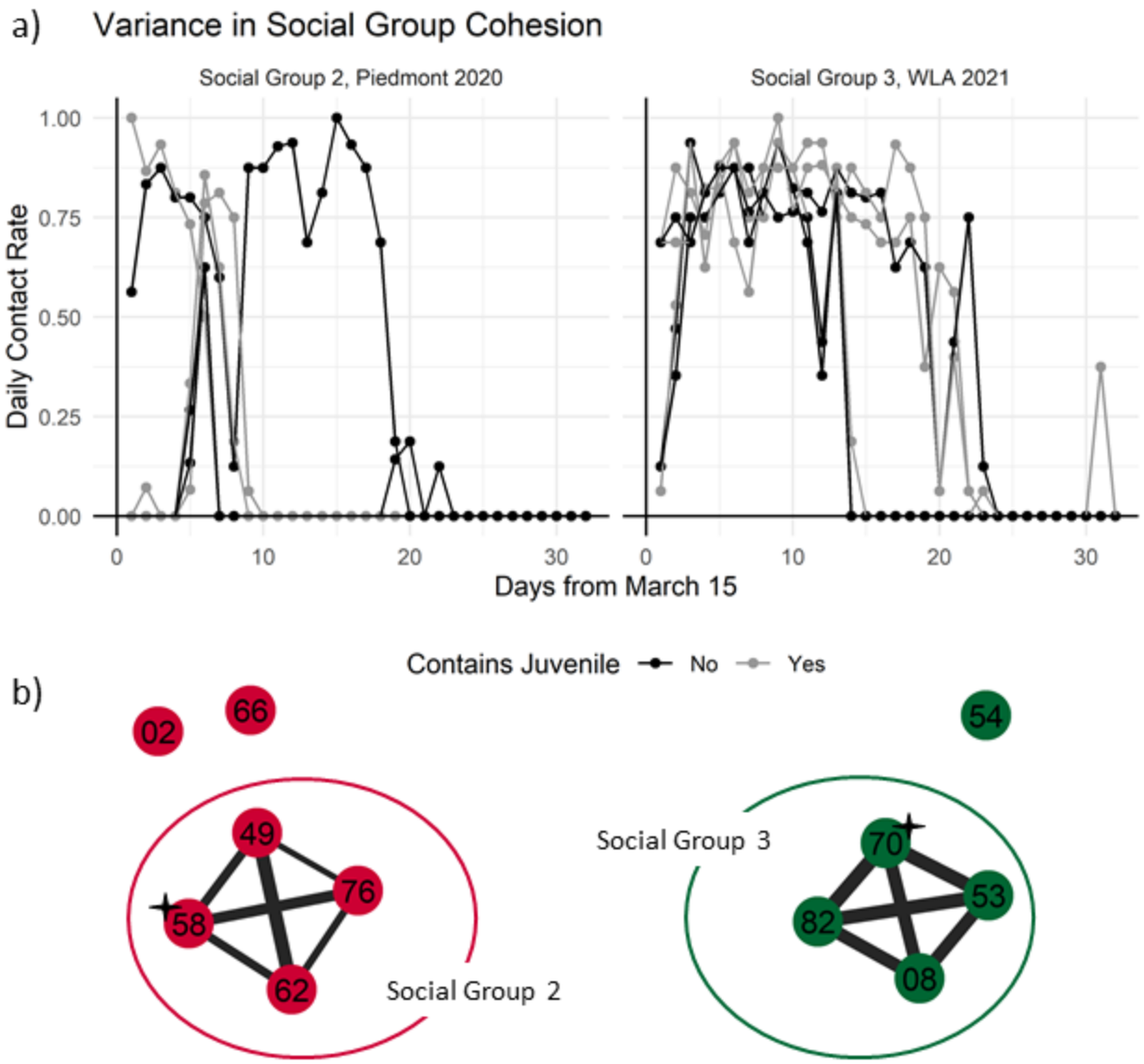

Figure 3.2: a) Daily contact rates for 2 social groups of female eastern wild turkey (*Meleagris gallopavo silvestris*) in the Piedmont (2020) and WLA (2021) regions of the southeastern United States during 2020-2021. Day is recorded on the x-axis as days from 15 March, and daily contact rate is recorded on the y-axis. Each line/point represents the daily contact rate for a dyad of females, and if that dyad contained at least one juvenile the color appears light gray. B) The weighted social network of each social group represented in Figure 3.2a. Red denotes females from Piedmont 2020 social group 2, and green denotes females from WLA 2021 social group 3.

Juveniles are marked with an asterisk. Lines connecting individuals are weighted to represent the total seasonal contact rate for each dyad.

CHAPTER 4

CONCLUSIONS

The eastern wild turkey (*Meleagris gallopavo silvestris*; hereafter, turkey) exhibits regional variations in fine-scale genetic structuring, which may be driven in part by habitat fragmentation, dispersal, kin clustering, and social behaviors. Prior to this work, there has been a paucity of information on population genetics and the genetic relationships among individuals within winter flocks. In addition, much of the prior research was limited to visual observations. Compared to other genetic techniques, population genomics has given researchers the ability to delineate fine-scale genetic structuring and calculate genetic relatedness among individuals. Concurrently, improvements to modern tracking technology using global positioning systems (GPS) are increasing our collective understanding of behavior, specifically social behaviors. Combining genomic and GPS data enabled me to explain broad and fine-scale genetic structuring of winter flocks, investigate kin clustering, and characterize sociality of female turkeys during the reproductive period.

Across 4 study regions and 3 states, I found variations in fine-scale genetic structure. Specifically, we noted high average relatedness in southeast Louisiana (r = 0.14) suggesting most members of a winter flock were related. Conversely, on a site in South Carolina (SC) not subjected to hunting pressure and harvest of males, I noted low average relatedness (r = 0.03), suggesting hunting may influence genetic structure at the population level. In addition, I noted average relatedness in winter flocks containing adult and juvenile females and some juvenile males (traditionally, a brood flock) was 63-78% lower in SC, suggesting increased natal

dispersal prior to winter flock formation. I offer that localized genetic differentiation is likely caused by constricted spatial structuring of related individuals. When considering the spatial clustering of relatives, relatives of the opposite sex generally were not within the same winter flock, and male coalitions had lower mean geographic distances compared to female coalitions in all regions except SC. With increasing rates of natural and anthropogenic landscape change, fine-scale population subdivision can be of conservation concern, as it is known to have negative impacts on reproduction and fitness. I suggest monitoring runs of homozygosity (ROH) in these populations to indicate if gene flow is experiencing bottlenecks or isolation processes.

I tracked temporal contacts rates between female turkeys to describe how social networks dissolve as females transition from winter flocks to pre-laying harems, and subsequently into laying/incubation ranges. I noted that social networks underlying female movements were complex and variable. Notably, I recorded a 95% decrease in sociality once females entered the laying period and that 94% of all social contacts occurred between unrelated individuals, suggesting females identify a cost to association with kin during the reproductive season. I suggest future research monitor female sociality year-round and across multiple years to investigate plasticity in female response to predation events and other stochastic processes. Furthermore, I offer that quantifying maternity and paternity within clutches in combination with spatial data and landscape variables could provide novel information on reproductive strategies used by wild turkeys.