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Research Article

Genetic analysis provides insight into the mating system of *Meleagris gallopavo* (Wild Turkey) and reveals frequent extra-pair paternity

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ABSTRACT

Lekking is a polygynous mating strategy where males gather on communal display grounds to attract females, who primarily visit these sites to mate. Females at leks are considered free to choose their mates, and only a few dominant males are expected to obtain most mating opportunities. *Meleagris gallopavo* (Wild Turkey) is a widely distributed, ground-nesting, uniparental galliform that exhibits a polygynous mating strategy, but aspects of the species' mating system are poorly understood. Our objective was to describe the mating system for *M. g. sylvestris* (Eastern Wild Turkey) using DNA extracted from eggshell membranes obtained from hatched clutches. We identified 307 offspring across 34 nests, assigned parentage, and examined sibling relationships among offspring. Our findings revealed that 19 (56%) nests had a single mother and father, whereas we detected multiple paternity in 15 (44%) nests. Additionally, we found that intraspecific nest parasitism occurred in 2.94% of nests, and we observed quasi-parasitism in only one nest containing an egg from an additional mother, indicating that parasitism is not a common alternative reproductive strategy represented in successful *M. g. sylvestris* nests. We observed that occurrences of multiple paternity were comparable to rates reported in other lekking species and suggest that multiple mating by females is an important alternative reproductive strategy for wild turkeys. Number of offspring sired by individual males increased with an increasing number of mates, and 6 males were responsible for 28% of all offspring, indicating a few males are most likely obtaining most mating opportunities. Our findings offer new insights into sexual selection and mating strategies of *M. gallopavo*.

Keywords: genetics, *Meleagris gallopavo*, multiple paternity, nest parasitism, parentage, polygyny

How to Cite

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LAY SUMMARY

- *Meleagris gallopavo* (Wild Turkey) is widely distributed across North America and aspects of their mating system are poorly understood.
- Male *M. gallopavo* attract and compete for females using gobbling and strutting behaviors. During the breeding season, male *M. gallopavo* attempt to mate with as many females as possible. Male *M. gallopavo* do not contribute any parental care, and females are considered free to choose their mates.
- We used genetic data extracted from hatched eggshells to assign parentage to offspring and examine sibling relationships within clutches.
- We detected multiple paternity in 44% of our nests and 56% were consistent with a single mother and father. Our findings offer new insights into mating strategies used by *M. gallopavo*.

El análisis genético aporta información sobre el sistema de apareamiento de Meleagris gallopavo y revela paternidad extra-pareja frecuente

RESUMEN

El lekking es una estrategia de apareamiento poligínica en la que los machos se reúnen en áreas de exhibición comunales para atraer a las hembras, quienes visitan principalmente estos sitios para aparearse. Se considera que las hembras en los leks son libres de elegir a sus parejas, y se

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espera que solo unos pocos machos dominantes obtengan la mayoría de las oportunidades de apareamiento. *Meleagris gallopavo* es un galliforme ampliamente distribuido, que anida en el suelo, presenta cuidado uniparental y exhibe una estrategia de apareamiento poligínica, pero los aspectos de su sistema de apareamiento son poco conocidos. Nuestro objetivo fue describir el sistema de apareamiento de *M. g. sylvestris* utilizando ADN extraído de membranas de cáscaras de huevos obtenidas de nidadas eclosionadas. Identificamos 307 crías en 34 nidos, asignamos la filiación parental y examinamos las relaciones de hermandad entre las crías. Nuestros hallazgos revelaron que 19 nidos (56%) tenían una sola madre y un solo padre, mientras que detectamos paternidad múltiple en 15 nidos (44%). Además, encontramos que el parasitismo intraespecífico del nido ocurrió en el 2,94% de los nidos, y observamos cuasi-parasitismo en un solo nido que contenía un huevo de una madre adicional, lo que indica que el parasitismo no es una estrategia reproductiva alternativa común en los nidos exitosos de *M. g. sylvestris*. Observamos que los casos de paternidad múltiple fueron comparables a las tasas reportadas en otras especies que forman leks y sugerimos que el apareamiento múltiple por parte de las hembras es una estrategia reproductiva alternativa importante en *M. gallopavo*. El número de crías engendradas por machos individuales aumentó con un mayor número de parejas, y 6 machos fueron responsables del 28% de todas las crías, lo que indica que unos pocos machos probablemente obtienen la mayoría de las oportunidades de apareamiento. Nuestros hallazgos ofrecen nuevas perspectivas sobre la selección sexual y las estrategias de apareamiento de *M. gallopavo*.

Palabras clave: filiación parental, genética, *Meleagris gallopavo*, parasitismo de nido, paternidad múltiple, poliginia

INTRODUCTION

Mating systems consist of behavioral strategies used by individuals to obtain mates (Johnson and Burley 1998) and are particularly relevant when attempting to understand patterns of sexual selection, as they influence variation in individual reproductive behaviors (Quader 2005). Fundamental aspects of mating systems, such as the number of mates per male and prevalence of multiple mating by females play a key role in determining the opportunity for sexual selection (Shuster and Wade 2003). However, ecological constraints, including spatial and temporal patterns of resource dispersion limit the extent to which sexual selection operates (Emlen and Oring 1977).

In a lek mating system, males congregate on communal display grounds to attract potential mates, and females visit leks solely for the purpose of mating. In polygynous mating system, males are often highly ornamented and do not provide parental care (Bradbury 1981). Females are considered free to choose their mates (Mackenzie et al. 1995), visiting leks over several days, before selecting and mating with a single male (Beehler and Foster 1988, Alatalo et al. 1996). Both male competition and female choice have been identified as creating highly skewed mating success among displaying males (Beehler and Foster 1988, Gibson 1996, DuVal and Kempenaers 2008), with 10–20% of males obtaining 70-80% of copulations (Wiley 1991).

At leks, females should choose to mate with males that increase the viability of their offspring and improve their fitness. Behavioral studies indicate that females visit one or more leks before mating once with a single male (Wiley 1991, Alatalo et al. 1996). However, these observations may not be reflective of all lekking species (Lanctot et al. 1997), as substantive rates of multiple paternity ranging from 6% to 60% have been reported in many lekking species (Semple et al. 2001, Lebigre et al. 2007, Krakauer 2008, Ryder et al. 2009, Lesobre et al. 2010). If female mate choice is not constrained, females should mate with the preferred male of their choice and, thus, would not need to mate with multiple males. However, females may be more likely to mate with multiple males when their preferred mate choice is unavailable due to interference from other males (Trail 1985), or if they are temporarily monopolized by other females (Petrie et al. 1992).

Meleagris gallopavo (Wild Turkey) is a precocial, ground-nesting, uniparental galliform that is widely distributed across North America. *Meleagris gallopavo* are sexually dimorphic, with males exhibiting phenotypic characteristics such as larger body size, colorful iridescent plumage, spurs, and dermal ornaments (Pelham and Dickson 1992). Male *M. gallopavo* use reproductive strategies where they compete for mating opportunities via visual (strutting) and acoustic (gobbles) behaviors to attract females, secure mating opportunities, and establish and maintain dominance hierarchies (Bevill 1973, Healy 1992). During the breeding season, male *M. gallopavo* attempt to mate with as many females as possible, and previous research has suggested that all males may attempt to mate, but only a few males are responsible for most copulations (Watts and Stokes 1971, Krakauer 2005).

Meleagris gallopavo appear to exhibit a polygynous mating strategy, where males contribute no parental care, and there is no social bond between males and females (Healy 1992). The mating system of the *M. g. silvestris* (eastern Wild Turkey) has been assumed to be non-lekking (Höglund and Alatalo 1995) and has previously been described as male dominance polygyny, with males forming dominance hierarchies that determine their access to groups of females (Eaton et al. 1976, Williams and Austin 1988). Conversely, *M. g. intermedia* (Rio Grande Wild Turkey) have been described as adopting a lek-like mating system (Watts 1968, Watts and Stokes 1971). The differences in organization of mating system may be partly determined by habitat-dependent spacing patterns of males and females, with larger male aggregations in more open landscapes and smaller groups in more forested landscapes (Watts and Stokes 1971). Historically, mating strategies of *M. gallopavo* have been determined based on direct physical observations. However, outside of observations of captive-reared birds (Healy 1992), there is only a single published study identifying parentage in offspring of *M. g. intermedia* (Krakauer 2008) based on introduced individuals in an urban environment. Specifically, Krakauer (2008) reported that multiple mating by females occurred in 45% of nests, suggesting that *M. g. intermedia* may be promiscuous rather than polygynous. Outside of these findings on a local population of the Rio Grande subspecies, the mating system of the *M. gallopavo* remains poorly understood.

Our objective was to describe the mating system of the *M. g. silvestris* (hereafter, wild turkey) across the southeastern United States using genetic data to assign parentage to offspring and examine sibling relationships within clutches. We hypothesized that instances of multiple paternity within clutches would be common. Specifically, we predicted the frequency of multiple paternity in wild turkey would be comparable to levels reported in *M. g. intermedia* and other polygynous species. Additionally, we hypothesized that dominance hierarchies in male wild turkey would lead to unequal reproductive success, defined as the number of offspring that a male sires. Specifically, we predicted most offspring would be sired by a limited number of males due to the reproductive advantages conferred by dominance, and strong sexual selection would lead to a pronounced reproductive skew.

METHODS

Study Area

We conducted research on study sites located in Georgia and South Carolina, USA. During 2021-2023, we conducted research on B. F. Grant and Cedar Creek Wildlife Management Areas (WMA), along with private lands adjacent to both properties located in the Piedmont region of Georgia. B. F. Grant WMA was a 4,613-ha area owned by the Warnell School of Forestry and Natural Resources at the University of Georgia and managed cooperatively with the Georgia Department of Natural Resources (GADNR). B. F. Grant WMA was dominated by loblolly pine (*Pinus taeda*) stands, agricultural lands, mixed pine-hardwood forest, and hardwood lowlands containing mostly oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), and hickory (*Carya* spp; Wakefield et al. 2020). Forest management was primarily through patch cuts, thinning, and prescribed fire. Cedar Creek WMA was a 16,187-ha area owned by the U. S. Forest Service (USFS) and managed in partnership between the USFS and GADNR. Cedar Creek WMA was composed of loblolly pine uplands, mixed hardwood-pine forests, and hardwood lowlands (Wakefield et al. 2020). Forests on Cedar Creek WMA were primarily managed through thinning and periodic (3–4 yr interval) dormant-season (January to March) prescribed fires. We considered B. F. Grant and Cedar Creek WMAs to be a single study site (hereafter, Georgia) during analysis, as these areas were only separated by 4.55 km.

During 2021–2023, we also conducted research on the Savannah River Site (SRS), a 78,000-ha tract owned and operated by the U.S. Department of Energy. The SRS was located on the Upper Coastal Plain and Sandhills physiographic provinces in Aiken and Barnwell counties in South Carolina, USA. Approximately 94% of SRS was forests dominated by loblolly pine, longleaf pine (*P. palustris*), and bottomland hardwood forests. The remaining forested areas included forested swamps, riparian areas, and mixed hardwood stands (Imm and McLeod 2005). Prior to 1951, most of SRS was maintained in agricultural fields or recently harvested timber (White 2005). The U.S. Department of Agriculture Forest Service has increased forest cultivation since 1952, resulting in increased wildlife populations (Imm and McLeod 2005, White 2005). Approximately 30% of SRS was managed for *Picoides borealis* (Red-cockaded Woodpecker), with prescribed fire applied on a 3–5 yr fire return interval.

Capture and Handling

We captured 100 males (Georgia = 46, South Carolina = 54; Table 1) and 238 females (Georgia = 113, South Carolina = 125; Table 1) using rocket nets baited with cracked corn during January to March, 2021–2023, at 55 trap sites (Georgia = 22, South Carolina = 33). We aged (juvenile or adult) each captured individual using the presence of barring on the 9th and 10th primary wing feathers and sexed them via coloration of their breast feathers (Pelham and Dickson 1992). We banded wild turkeys with a uniquely identifiable aluminum rivet tarsal band (National Band and Tag Company, Newport Kentucky) and collected blood samples from the brachial or medial metatarsal vein of each captured individual. We transferred blood to either a microcapillary tube that contained lysis buffer (100 mM Tris, 100 mM EDTA, 10 mM NaCl, 2% SDS) or onto Whatman FTA cards that were stored at room temperature until DNA extraction.

TABLE 1. Number of male and female *Meleagris gallopavo silvestris* (Eastern Wild Turkey) captured and fitted with a transmitter on B.F. Grant and Cedar Creek Wildlife Management Areas in Georgia and the Savannah River Site, South Carolina, USA, 2021–2023.

	Georgia		South Carolina	
	Male	Female	Male	Female
2021	13	35	20	47
2022	14	44	17	43
2023	19	34	17	35
Total	46	113	54	125

In 2021, we fitted all individuals with a backpack style Global Positioning System/Very High Frequency (GPS/VHF) transmitter (Biotrack Limited, Wareham, Dorset, UK; Guthrie et al. 2011). We programmed GPS units to record hourly locations from 5:00 to 20:00 with one location nightly (23:59:58; Cohen et al. 2018). From 2022 to 2023 we fitted all individuals with a GPS/ACC/UHF transmitter (E-obs GmbH; Munich, Germany). We programmed GPS units to collect data from 4:00 to 20:00 daily. All units collected data from the day of capture until the battery died (~9 months to 1 yr) or until the unit was recovered. We released individuals at the capture location following processing.

Nest Monitoring and Eggshell Collection

We monitored live-dead status and general movements of female wild turkeys ≥2 times per week during the reproductive season using a 3-element handheld Yagi antenna and receiver. We remotely downloaded GPS data from each wild turkey once per week via VHF/UHF handheld command unit receivers. We spatially projected GPS locations in ArcGIS 10.8 (Environmental Systems Research Institute, Redlands, California, USA) to identify nest locations by determining when a female's locations became concentrated around a single area for several days (Guthrie et al. 2011, Conley et al. 2015, Yeldell et al. 2017, Wood et al. 2019). Nesting females were not disturbed or flushed from nest sites during monitoring but were instead live-dead checked daily via VHF/UHF from a distance >20 m. Wild turkey nests require ~27 days of continuous incubation before hatching (Williams et al. 1971), but incubation can vary from 25 to 29 days (Healy and Nenno 1985). When GPS locations indicated nest termination, we visually located nest sites to confirm the estimated nest location and determine nest fate. Genetic samples of offspring were obtained by salvaging eggshell membranes from hatched nests (Pearce et al. 1997, Strausberger and Ashley 2001). We considered nests as hatched if the eggshells had a distinct pipping around the top of the egg with the egg top still attached via the membrane and laying within the nest bowl. All membranes were placed in individual paper bags with a uniquely identifying label and frozen until processing.

Hatched eggshell membranes were processed by extracting the vascularized chorioallantois membrane, placing these membranes in 0.5 M EDTA, and then in an incubator set at 56 °C for 8–12 hr. We then macerated vascularized chorioallantois membranes with forceps and scalpels. We preserved macerated membrane samples in 300 μL of lysis buffer (100 mM Tris, 100 m EDTA, 10 mM NaCl, 2% SDS), which stabilized the solution and allowed for room temperature storage and shipment of samples.

DNA Extraction and Genotyping

Genotyping-in-Thousands by sequencing (GT-seq; Campbell et al. 2015) is a type of amplicon sequencing that involves the development of multiplexed polymerase chain reaction (PCR) primers that target 50 to 1,000 pre-identified loci. GT-seq panels require previous identification of loci of interest, typically generated through restriction-site associated DNA sequencing (RADseq) or other approaches using high-quality DNA samples. A previous RADseq single-nucleotide polymorphism (SNP) dataset ($n = 358{,}094$; Watkins et al. 2025) was used to select candidate loci for GT-seq panel development. Blood and hatched eggshell samples were then sent to GT-seek LLC (https://gtseek.com/) for primer design and genotyping. Genomic DNA was extracted from blood samples using a Chelex extraction protocol and from eggshell membrane samples in lysis buffer using a ProK/Chelex digest followed by a magnetic bead cleanup (Walsh et al. 1991). Samples used in primer and panel development for our study were chosen to avoid ascertainment bias and be representative of the populations, with locus selection based on a combination of high F_{ST} and high heterozygosity markers.

Library construction followed the GT-seq protocol described in Campbell et al. (2015) and modified to include the Nate's Plates PCR normalization and tagging kit (https://gtseek.com/product/natesplate96w10/). For PCR amplification of target loci from blood samples, we added 2 µL of input gDNA template, 3.5 µL Qiagen Plus multiplex master mix, and 1.5 µL of pooled primer mix. Thermal cycling conditions were: hot start of 95 °C for 15 min; 5 cycles (95 °C for 30 s, 5% ramp down to 57 °C for 30 s, 72 °C for 2 min); 10 cycles (95 °C for 30 s, 65 °C for 30 s, 72 °C for 30 s) 4 °C final hold. This PCR product was diluted 20-fold, and 3 µL was combined with 2 µL of Qiagen Plus multiplex master mix in a new 96-well Nate's Plate for the indexing reaction. Thermal cycling conditions for the indexing PCR were 95 °C for 15 min; 10 cycles (95 °C for 10 s, 65 °C for 30 s, 72 °C for 30 s); 72 °C for 5 min, 4 °C hold. The purified libraries were then eluted with 15 µL nuclease-free TE pH 8.0 and transferred to fresh 1.5-ml tubes before adding 1.5 µL EB with 1% Tween-20. Following bead size selection and purification, libraries were quantified by qPCR using duplicate dilutions of 1:1,000, 1:2,000, 1:4,000, and 1:8,000.

The GT-seq bioinformatics pipeline on GitHub (https://github.com/GTseq/GTseek_utils) was used to process raw sequencing reads into individual *fastq* files (*GTseq_Genotyper_v3.pl*). Genotypes for each locus were called based on the percentage of allele 2 reads, where allele 2 percentages ≤10% were homozygous for allele 1, allele 2 percentages between 30% and 70% were called heterozygous, and allele 2 percentages above 90% were homozygous for allele 2. Loci with < 10 reads were not genotyped (Campbell et al. 2015). Panel optimization was largely guided by the outputs of *GTseq_PrimerTest.pl* and *GTseq_Primer-Interaction-Test_v3.pl*; the former identified over-represented primers based on the proportion of total reads that contained a forward primer or reverse primer sequence, whereas the latter identified primers responsible for copious primer-dimers or undesirable PCR artifacts. After excluding loci with undesirable characteristics, 360 SNPs remained for inclusion in the GTseq panel.

When comparing GT-seq genotypes to GT-seq genotypes the concordance rate was high (99.5%+). While technical replicates were not included to estimate the rate of genotyping error, several individuals appeared to have been sampled more than once in the field, resulting in matching genotypes across samples. These matching genotypes indicate that the error rate was low when genotyping identical samples.

Genetic Analysis, Parentage, and Sibling Relationships

Genetic samples with >20% missing data (–geno 0.20) and SNPs with >10% missing data (–mind 0.10) were removed using PLINK v1.90b6.17 (Purcell et al. 2007). We generated a statistically unlinked and neutral set of SNP loci by removing SNPs with minor allele frequency (MAF) below 20% (–maf 0.20) and removing SNPs based on inter-locus genotype correlations as a proxy for linkage disequilibrium (LD; –indep-pairwise), which left us with 259 SNPs for analysis.

To ensure data quality we excluded any clutches for which we were unable to genotype more than 2 eggshells. Wild turkey clutches have fertility rates of ~88%; therefore, it is plausible that 1–2 eggs may be infertile in a typical clutch (Vangilder 1992) and fail to yield embryonic tissue. For example, a clutch with 5 eggshells would be included if at least 3 eggshells were successfully genotyped. Likewise, smaller clutches with 2 or 3 offspring were retained if all or all but one offspring were genotyped. This threshold was applied to reduce the influence of incomplete clutches, while retaining as many clutches as possible with adequate genotyping success.

We quantified relationships among nesting females and each of their clutches in the program COLONY v. 2.0.6.5 (Jones and Wang 2010). COLONY implements full-pedigree likelihood methods to simultaneously infer sibship and parentage among individuals using multilocus genotype data. A pairwise likelihood approach, most commonly used in CERVUS 3.0 (Kalinowski et al. 2007), is often used to assign parentage in wild populations, but COLONY has been found to make fewer errors in assignment compared to CERVUS for populations with female kin structure and partial sampling of mothers (Thow et al. 2022). However, incorrect assignment of offspring from nesting females to other females with either program is rare (Thow et al. 2022).

To accurately assign parentage of offspring within a nest, we assigned maternity to incubating females. We assumed the GPS marked female incubating a given clutch was the genetic mother of offspring from that nest. COLONY infers paternal lineages across samples, providing the ability to assess the number of sexual mates present in assessed clutches. We specified no known siblings, no excluded sibships, and no sibship size prior. We allowed a polygamous mating system for both males and females. We conservatively set the probability that a mother was included in the female candidates to 0.55, to allow for high numbers of un-captured, un-sampled exclusive parasite females. Setting this parameter lower than the true probability may reduce COLONY's reported confidence in an individual assignment but does not change the identity of the assigned parents (Thow et al. 2022). We selected the longest processing run option, using full-likelihood approach, with 4 replicates to reduce sampling bias (Thow et al. 2022). We excluded parental, full-sibling, and half-sibling dyads with COLONY assigned relationship probabilities <20% as the mean probability of assignment was 96%. In addition to running an analysis in which offspring and mothers were compared, we also ran all mothers in a single analysis to determine the number of related females in the dataset. We ran each study site separately.

RESULTS

We collected eggshell samples from 73 hatched nests with 720 offspring. We excluded 258 offspring from which no DNA was genotyped and used 34 nests (Georgia = 9, South Carolina = 25) with 307 (Georgia = 66, South Carolina = 241) genotyped offspring for analysis (Table 2). Of these 34 nests, 18 were classified as complete clutches, meaning all eggshells collected from the nest were successfully genotyped (see Supplementary Material for results using the full dataset). We identified 34 mothers (Georgia = 9, South Carolina = 25) with an average of 8.77 offspring per nest (SD = 3.48, Range 1–14). We assigned paternity for 60 (Georgia = 18, South Carolina = 42) of 307 offspring to males we captured during trapping, whereas the remaining 247 offspring were sired by unsampled males (Figures 1 and 2).

We found that 19 nests (56%, Georgia = 2, South Carolina = 17) were consistent with a single mother and father. We detected multiple maternity in one nest (out of 34, 2.94%). Within the nest only one egg was from a female other than the incubating female and the individual was sired by the same male that sired other offspring, indicating quasi-parasitism occurred. Notably, the incubating female and parasitic female were half-siblings.

We detected multiple paternity involving 2 or more males in 15 nests (44%, Georgia = 6, South Carolina = 9). We found 7 males sired offspring in more than one nest (Georgia = 2, South Carolina = 5). Mean number of offspring per male was 7.31 (SD = 4.56, range = 1–19), and the average number of males represented per nest was 1.47 (SD = 0.56, range = 1–3). We found that across all sires (both sampled and unsampled) 6 males (14%, Georgia = 1, South Carolina = 5), were responsible for siring 86 offspring (28%, Georgia = 12, South Carolina = 74; Figure 3).

Only one pair of females who were identified as mothers were found to be full siblings (South Carolina = 1), and 3 pairs of females were identified as half siblings (Georgia = 2, South Carolina = 1). Sibling relationships across offspring consisted of 1,141 full sibling dyads (Georgia = 202, South Carolina = 939; Figures 4 and 5) and 361 half sibling dyads (Georgia = 73, South Carolina = 288). Specifically, we found that 74.5% of offspring were full siblings (Georgia = 73.45%, South Carolina = 74.70%), indicating these individuals shared both a

TABLE 2. Parentage assignment for *M. g. silvestris* (Eastern Wild Turkey) offspring on B.F. Grant and Cedar Creek Wildlife Management Areas in Georgia and the Savannah River Site, South Carolina, USA from 2021–2023.

Year	Number of offspring	Number of nests	Number of sampled fathers	Number of inferred fathers	Number of sampled mothers
2021	70	8	1	8	8
2022	188	19	3	23	20
2023	49	7	3	5	7
Total	**307**	**34**	**7**	**36**	**35**

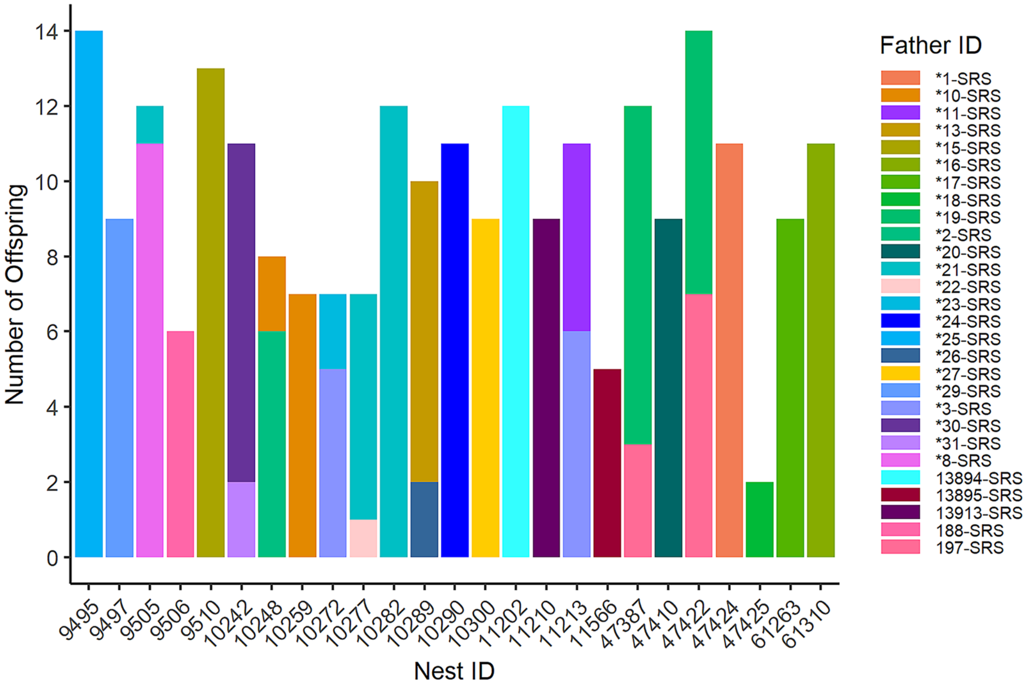

FIGURE 1. Number of eastern wild turkey (*Meleagris gallopavo silvestris*) offspring for each nest on the Savannah River Site in South Carolina, USA during 2021–2023. Each bar represents a single nest, with stacked segments indicating the number of offspring sired by each male. Color corresponds to individual Father IDs and tick marks along the x-axis correspond to unique nests. In the legend, Father IDs with an asterisk were unsampled males.

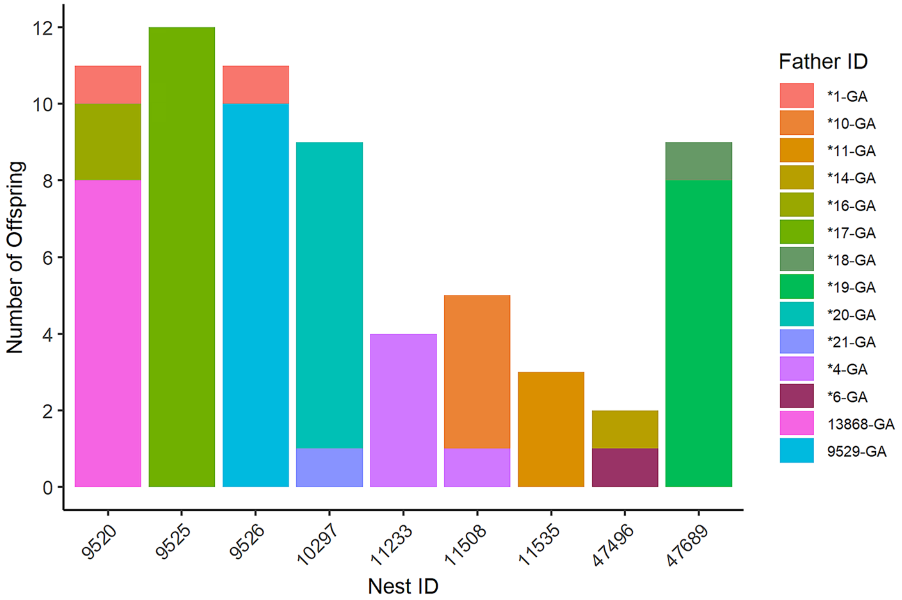

FIGURE 2. Number of eastern wild turkey (*Meleagris gallopavo silvestris*) offspring for each nest on B.F. Grant and Cedar Creek Wildlife Management Areas in Georgia, USA during 2021-2023. Each bar represents a single nest, with stacked segments indicating the number of offspring sired by each male. Color corresponds to individual Father IDs and tick marks along the x-axis correspond to unique nests. In the legend, Father IDs with an asterisk were unsampled males.

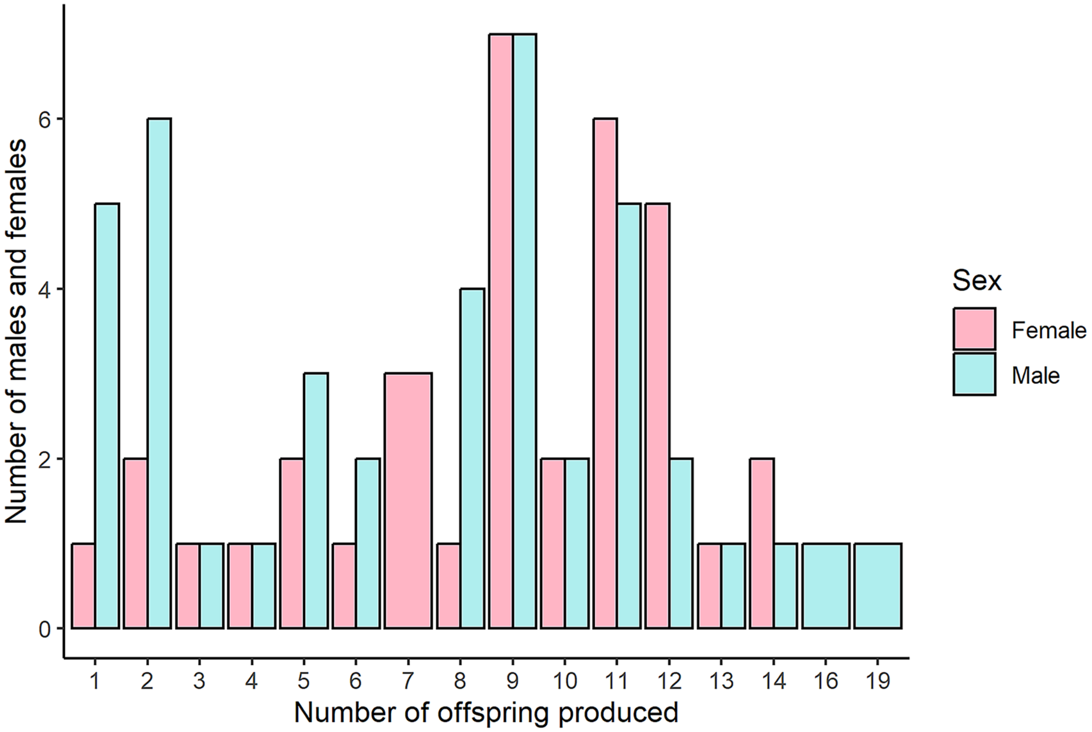

FIGURE 3. Distribution of offspring produced by male and female eastern wild turkeys (*Meleagris gallopavo silvestris*) across B.F. Grant and Cedar Creek Wildlife Management Areas in Georgia and Savannah River Site in South Carolina, USA during 2021-2023. Bars represent the count of males (blue) and females (pink) with varying numbers of offspring.

mother and father, whereas 25.5% of offspring were half siblings (Georgia = 26.55%, South Carolina = 25.30%), suggesting these individuals shared only a single parent. Additionally, 134 of the 288 half-sibling dyads in South Carolina and 7 of the 73 half-sibling dyads in Georgia shared the same father, whereas 154 half-sibling dyads in South Carolina and 70 half-sibling dyads in Georgia shared the same mother.

DISCUSSION

Mating strategies are fundamental to understanding the demographics, genetic diversity, and evolutionary dynamics of a species (Emlen and Oring 1977, Quader 2005). Understanding reproductive strategies provides insights into interpreting broader population processes (Johnson and Burley 1998). We sought to investigate reproductive strategies used as part of the

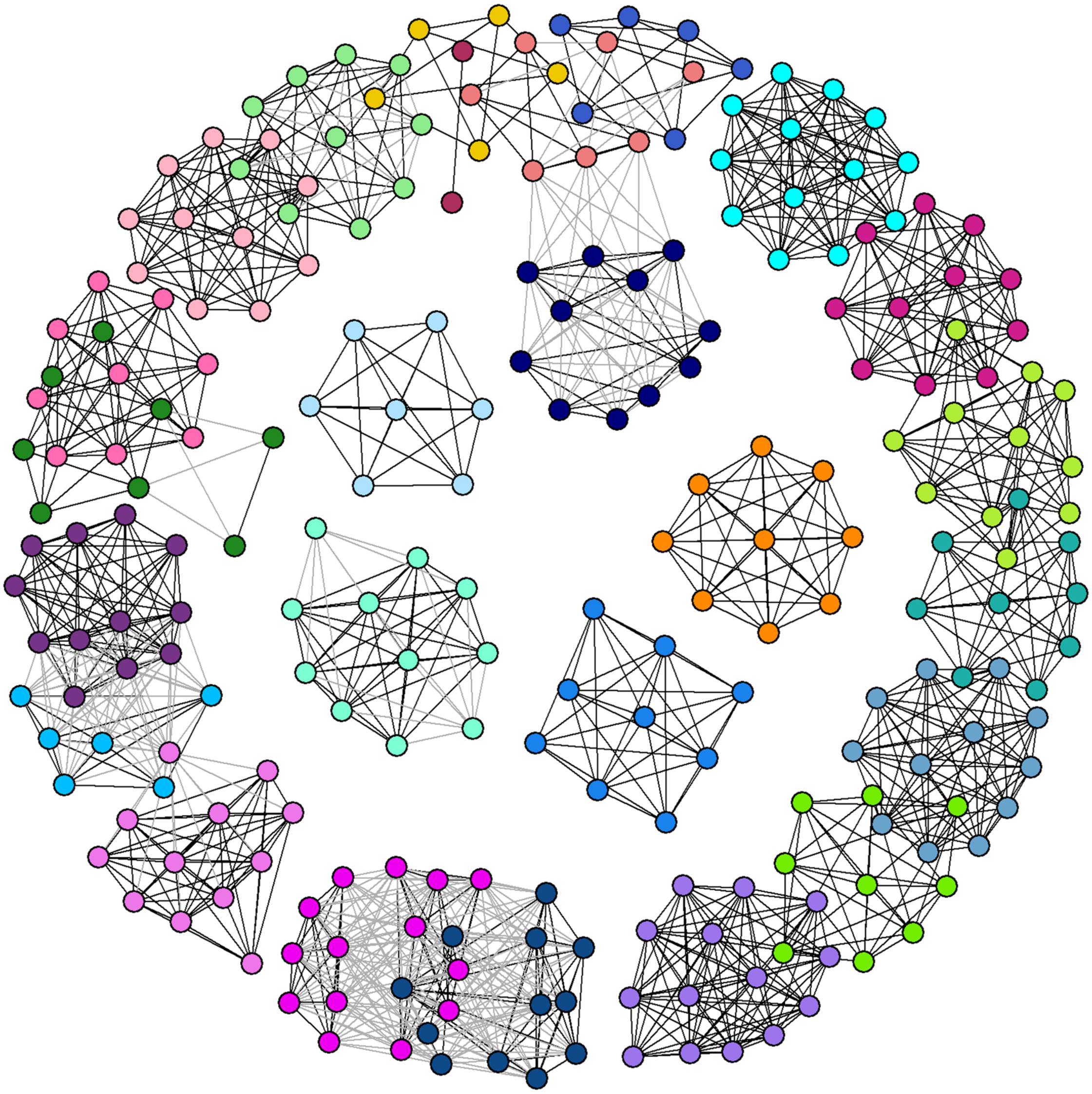

FIGURE 4. Network of sibling relationships among eastern wild turkey (*Meleagris gallopavo silvestris*) offspring across 25 hatched clutches on the Savannah River Site in South Carolina, USA during 2021-2023. Each node represents an individual offspring, and each cluster represents siblings within a nest. Nodes are colored according to the clutch from which they belong. Solid black edges indicate full-sibling relationships, whereas gray edges indicate half-sibling relationships. The layout positions cluster to illustrate the connectivity of siblings across clutches, with closely related individuals forming tight clusters.

wild turkey mating system (Krakauer 2008). We used DNA extracted from eggshell membranes to describe the mating system of the wild turkey through assigning parentage of offspring and examining sibling relationships within clutches. We found evidence of both multi-paternity and multi-maternity in clutches of wild turkey, along with evidence that a few males may be responsible for the majority of offspring. Our findings contribute to broader contemporary literature demonstrating the use of alternative reproductive strategies in Galliformes and lekking species.

In species where there is potential for multi-parentage, genetic analyses are crucial to accurately estimate male reproductive success (Coltman et al. 1999, DeWoody 2005, Deyoung and Honeycutt 2005). We observed a frequency of multiple paternity comparable to 45% reported in a *M. g. intermedia* population (Krakauer 2008) and 40% in species such as *Tryngites subruficollis* (Buff-breasted Sandpipers; Lanctot et al. 1997) and 60% in *Chlamydotis undulata undulata* (Houbara Bustard; Lesobre at al. 2010), species who use a polygynous mating system centered around exploded leks. Conversely, the rates of multiple paternity we observed were higher than those reported in classical lekking species, such as *Centrocercus urophasianus* (Greater Sage-Grouse; Semple et al. 2001, Bird et al. 2013), where female grouse are primarily monogamous (Alatalo 1996). We found that multiple paternity occurred in 44% of nests, suggesting that multiple paternity is an important component of mating strategies used by female wild turkeys (Krakauer 2008). However, we recognize that our estimates of multiple paternity may be underestimated as we could not always be certain that we collected every eggshell laid by an incubating female. Lekking species have been characterized as having low rates of multiple paternity based on the logic that multiple mating is unnecessary because of unconstrained female mate choice, and highly attractive males are available to all females (Westneat 1990). Multiple mating may occur because of a female's preference for particular males, as females that mate with a non-preferred male are more likely to mate again with another male (Petrie et al. 1992). It is plausible that given

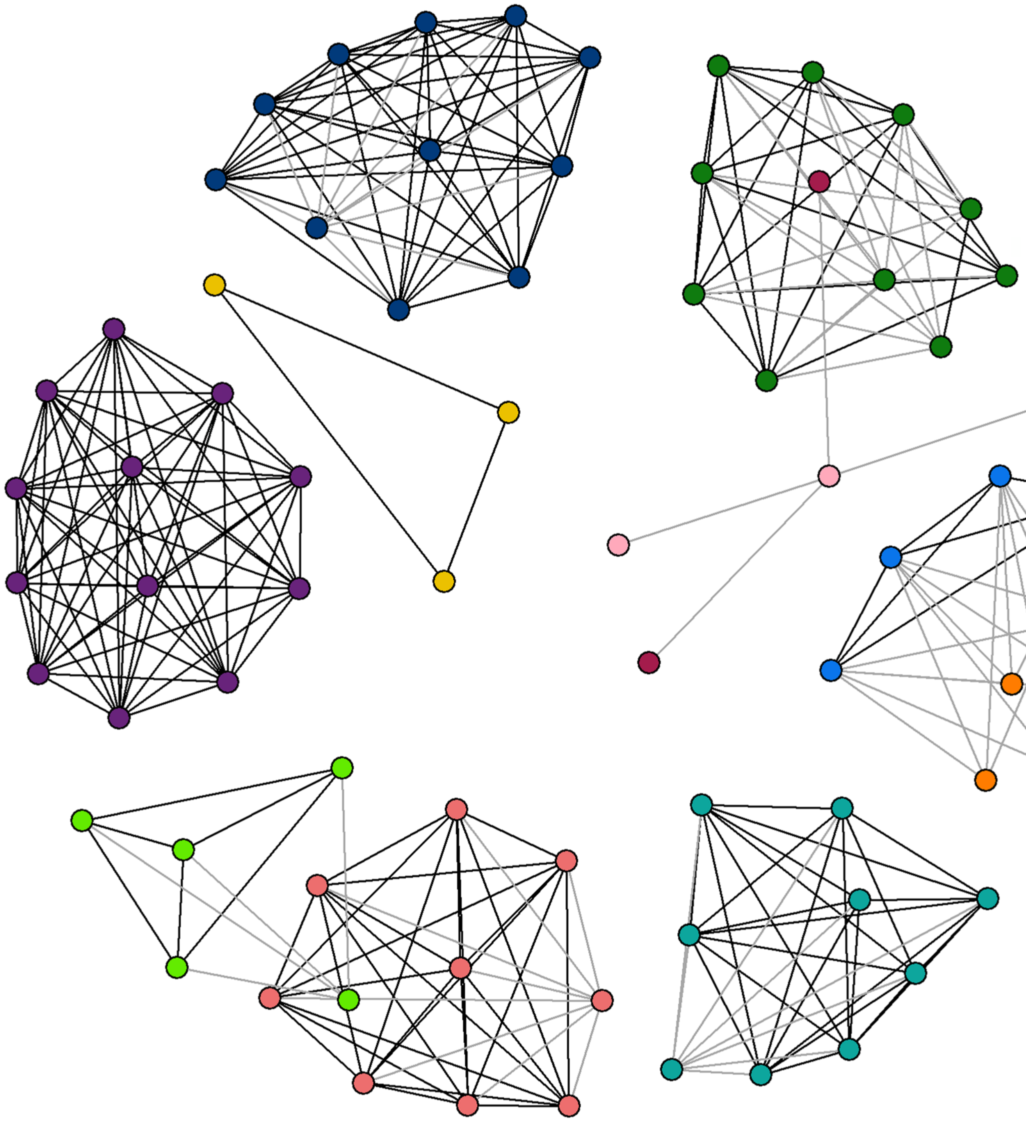

FIGURE 5. Network of sibling relationships among eastern wild turkey (*Meleagris gallopavo silvestris*) offspring across 9 hatched clutches on B.F. Grant and Cedar Creek Wildlife Management Area in Georgia, USA during 2021–2023. Each node represents an individual offspring, and each cluster represents siblings within a clutch. Nodes are colored according to the nest from which they belong. Solid black edges indicate full-sibling relationships, whereas gray edges indicate half-sibling relationships. The layout positions cluster to illustrate the connectivity of siblings across nests, with closely related individuals forming tight clusters.

the low cost to females of mating with multiple males (Gibson and Bachman 1992), females may adopt this strategy to obtain potential genetic benefits including sperm competition, sperm selection (Yasui 1998), or bet hedging to guarantee successful inseminations (Kempenaers and Dhondt 1993, Krokene et al. 1998).

In lek mating systems, females are presumed to base mating decisions on obtaining superior genes for their offspring (Höglund and Alatalo 1995). Females within a flock may use the same cues to assess and select the same males, indicating a consensus in female mate choice (Birkhead and Møller 1992, Höglund and Alatalo 1995, Mackenzie et al. 1995). We found that 14% of males were responsible for siring 28% of all offspring. Furthermore, in South Carolina, 46.5% of the half siblings shared a father, indicating that multiple mating by females occurred, but some males sired more offspring than others. Conversely, in Georgia, only 9.6% of half-siblings shared fathers, suggesting paternity was more evenly distributed. For each additional mate a male wild turkey acquired, his reproductive success increased by ~4 offspring, implying that males with higher mating success would have disproportionately higher reproductive success. Similarly, Krakauer (2008) found males experienced a significant gain in reproductive success from additional mates. However, because we were unable to sample every nest across our landscape and if males that we already identified sired offspring in unsampled nests, our estimate of reproductive success would be underestimated (Møller and Ninni 1998, Freeman-Gallant et al. 2005). Additionally, if offspring were sired by unknown fathers in nests that were unsampled, reproductive success could decrease. Although, it is likely that both of these processes occurred and offset each other to some extent, suggesting that our estimates of reproductive success were reasonable but should be investigated further.

Intraspecific nest parasitism has been described in 32 species of Galliformes (Yom-Tov 2001). Various accounts have documented cases of intraspecific nest parasitism in Wild turkey using photographic evidence (Brautigam et al. 2016), inferences made from GPS and telemetry data, (Sullivan et al. 2022), and molecular genetics (Krakauer 2008), with these accounts suggesting that instances of intraspecific nest parasitism are minimal in *M. gallopavo*. We provide further evidence that intraspecific nest parasitism occurs at relatively low levels (2.94%). We note that our estimates were lower than rates documented in a *M. g. intermedia* population using molecular genetic data (Krakauer 2008) and rates estimated to occur in populations of eastern and *M. g. intermedia* based on inferences made from GPS locations (Sullivan et al. 2022). Furthermore, the rates of intraspecific nest parasitism we observed were lower than rates of 26.9% reported in *C. u. undulata* (Lesobre et al. 2010), 21% in *Colinus virginianus* (Northern Bobwhite Quail; Davis et al. 2017), and 9.6% reported in *Centrocercus urophasianus* (Bird et al. 2013). We also observed an instance of quasi-parasitism, and in this instance the incubating female and parasitic female were half siblings. However, the parasitic female did not initiate her own nest, so we speculate that relatedness between host and parasite may have provided inclusive benefits to both the incubating and parasitic female (Andersson et al. 2019).

Meleagris g. sylvestris and *M. g. intermedia* inhabit a diverse array of vegetative communities throughout their range but share important similarities in that males do not provide parental care, and there is no social bond between males and females. Extant literature has characterized the mating system of *M. g. sylvestris* as using male dominance polygyny (Eaton et al. 1976, Williams and Austin 1988) and *M. g. intermedia* as lekking (Watts and Stokes 1971). However, coupled with earlier findings detailing genetics of the mating system on a population of *M. g. intermedia* (Krakauer 2008), our findings suggest that prior characterizations were inaccurate, as it appears that both subspecies use similar mating strategies. We recommend additional research examining parentage across wild turkey subspecies and across other parts of the species' geographic range. We encourage research to further explore potential mechanisms to explain why multiple paternity and intraspecific nest parasitism strategies are used by *M. gallopavo*, and additional fitness consequences of adopting these strategies. Additionally, we suggest future research examine potential influences of multiple paternity and intraspecific nest parasitism on brood survival and success.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

All wild turkey capture, handling, and marking procedures were approved by the Institutional Animal Care and Use Committee at the University Georgia (Protocol #A2019 01-025-R2 and A2020 06-018-R1).

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

EEU: Data curation; Formal analysis; Investigation; Methodology; Software; Writing-original draft. PEG: Data curation; Investigation; Writing-review & editing. SAW: Data curation, Investigation; Methodology; Writing-review & editing. NWB: Data curation; Formal Analysis; Investigation; Writing-review & editing. JCK: Project administration; Resources; Writing-review & editing. PL: Methodology; Software; Validation; Writing-review & editing. HMB: Methodology; Software; Validation; Writing-review & editing. BAC: Conceptualization; Methodology; Writing-review & editing. MJC: Conceptualization; Funding acquisition, Methodology, Project administration, Supervision, Writing-review & editing.

Data availability

Analyses reported in this article can be reproduced using the raw data provided by Ulrey et al. (2025).

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