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# The Mating System of White-Tailed Deer Under Quality Deer Management

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**ABSTRACT** Mating systems, which can reveal temporal and spatial plasticity within a given species, may influence inbreeding, effective population size, genetic diversity, reproductive fitness, and survival. Although observational research on white-tailed deer has indicated dominant males monopolize breeding opportunities, recent molecular studies suggest a more complex system. It is possible that population characteristics fostered under management strategies designed to balance the sex ratio and extend the male age structure, such as Quality Deer Management (QDM), influence the pre-breeding interactions that affect the distribution of mating success across age classes. Therefore, our objective was to evaluate the white-tailed deer mating system under QDM through paternity analysis. Using 8 microsatellite loci and tissue samples harvested from hunter-killed deer at Chesapeake Farms in Chestertown, Maryland, we evaluated 731 deer. The ≥3.5 age class dominated mating at Chesapeake Farms, with 41% of paternity. However, together, the 1.5- and 2.5-year-old age classes accounted for more than half of paternity (59%). No evidence of polyandry was detected. Our results indicate the interaction between the sex ratio and age structure, fostered by strategies that balance the sex ratio and extend the male age structure, facilitate breeding by younger males. These results indicate management strategies that employ QDM practices with a goal of propagating the genes of dominant males may fall short, and the interplay among sex ratio, age structure, and dominance relationships may be the main influences of mating success. Managers should account for these findings when setting expectations for reproduction under restricted harvest. © 2016 The Wildlife Society.

**KEY WORDS** Chesapeake Farms, microsatellite profiling, *Odocoileus virginianus*, paternity analysis, Quality Deer Management, white-tailed deer.

Advances in molecular DNA technologies enhanced the understanding of mating systems by allowing biologists to test observation-based hypotheses about mating systems and reproductive success in natural populations (Jones et al. 1999, Worthington Wilmer et al. 1999, Garnier et al. 2001, Booth et al. 2007, DeYoung et al. 2009). Within a given species, plasticity in the mating system may exist spatially and temporally (Apollonio et al. 1992, Rowe et al. 1994, Mobley and Jones 2007) and may influence levels of inbreeding (Stockley et al. 1993), effective population size (Sugg and Chesser, 1994, Parker and Waite 1997), reproductive fitness (Thirgood 1991), and potentially survival (Beehler and

Foster 1988). As such, for species of economic importance or conservation concern, an accurate understanding of mating strategies may benefit the formulation of effective management decisions (Clutton-Brock 1989, Garnier et al. 2001, Festa-Bianchet 2003).

The mating system of white-tailed deer (*Odocoileus virginianus*) is characterized by polygyny, wherein a single male forms a tending bond with a single female, courting, guarding, and ultimately mating with her during estrus (about 24 hr but possibly as long as 48 hr; Haugen 1959, Michael 1966, Moore and Marchinton 1974, Knox et al. 1988) before moving to another female (Hirth 1977, Marchinton and Hirth 1984, Clutton-Brock 1989, Holzenbein and Schwede 1989). Although observational research on white-tailed deer has indicated dominant males monopolize breeding opportunities (Hirth 1977, Marchinton and Hirth 1984), recent molecular work suggests a more complex system, with younger

males successfully siring offspring (Sorin 2004, DeYoung et al. 2006, DeYoung et al. 2009). Therefore, the mating system may facilitate breeding by non-dominant males who have access to untended females and polyandry if tending males are displaced and sperm mixing occurs (Hirth 1977, Clutton-Brock 1989). Given the demands of the tending bond and the scattered spatial distribution of females, it is unlikely that dominant males could completely monopolize breeding in free-range populations (Sorin 2004; DeYoung et al. 2006, 2009). Additionally, yearling males continue to spar after breeding begins and chase females when dominant males are otherwise occupied, suggesting they do contribute to breeding (Hirth 1977, Ozoga and Verme 1985); however, the contribution of these younger males in mixed-age populations is unknown.

Population characteristics may further influence the pre-breeding interactions that appear to affect the distribution of mating success. Deer managers are increasingly implementing strategies designed to influence population dynamics through harvest restrictions (Newsom 1984, Woods et al. 1996). Quality Deer Management (QDM) and related strategies are characterized by increased female harvest and restraint in harvesting young males (Hamilton et al. 1995, Shaw 2005), resulting in older male age structure, a more balanced sex ratio, high estrous synchrony, and a reduced population density. Although the interaction between age structure and sex ratio is unclear and intraspecific mating systems may vary (Clutton-Brock 1989, Thirgood 1991, DeYoung et al. 2009), the characteristics of QDM could influence the mating system of white-tailed deer by reducing reproductive success per male and across age classes (Langbein and Thirgood 1989, Festa-Bianchet 2003). Also, the younger female age structure achieved under such systems possibly affects mating.

Although polyandry has been documented in captive white-tailed deer (DeYoung et al. 2002, 2006; Sorin 2004), the factors influencing polyandry are unclear. For example, DeYoung et al. (2002) detected no clear relationship between sex ratio and polyandry. However, high estrous synchrony, as observed in northern latitude populations and in those populations under QDM, may negatively influence polyandry through shortened competition for estrous females. Conceivably, the sex ratio and male age structure fostered by restrained male harvest could affect and possibly heighten competition for mates, which in turn may affect mating strategies and levels of polyandry. Our objective was to use molecular methods to understand the effects of age class on male mating success in a population of white-tailed deer managed under QDM by assigning parentage. We hypothesized that younger male age classes would contribute substantially to mating under a system with a broad age structure and balanced sex ratio, suggesting a variety of behavioral strategies can lead males to breeding success.

## STUDY AREA

Chesapeake Farms is a 13-km² property on Maryland's Eastern shore comprising 50% forest with non-alluvial swamps, 20% cropland, 13% fallow fields, and 17% composed of impoundments and other managed wildlife habitat (see Shaw 2005, Karns et al. 2011 for additional detail). The white-tailed deer population, hunted annually for at least 40 years, was managed under QDM beginning in 1994. Harvest of males during our study period was restricted to individuals with antler spreads wider than ear tips (i.e., ≥2.5 years old; see Table S2, available online at www.onlinelibrary.wiley.com). The male:female sex ratio was 1:1.25 for the duration of the study with density of approximately 30 deer/km² in 2003, 25 deer/km² in 2004–2007, and 33 deer/km² in 2008–2009, yielding estimated populations of 390 individuals in 2003, 325 in 2004–2007, and 429 in 2008–2009 (M. C. Conner, Chesapeake Farms, unpublished data). Mean population size for the duration of the study was 364 individuals (M. C. Conner, unpublished data).

## METHODS

We collected tongue tissue from male and female deer harvested at Chesapeake Farms between 2002 and 2009. We recorded sex and age; animals were aged using tooth wear and replacement employing a set of known-age jaws collected onsite for comparison (Severinghaus 1949). We collected ear tissue biopsies from adult males collared for unrelated studies and fawns that were captured each spring as part of routine tagging efforts at Chesapeake Farms and tissue samples from fetuses when available in harvested females (e.g., taken in spring). We sampled 731 individuals for parentage analysis: 230 male, 501 female. We extracted DNA from tissue samples following an adaptation of the PureGene DNA isolation protocol (Gentra Systems, Minneapolis, MN, USA). We genotyped samples using a panel of 8 microsatellite loci (D, K, N, P, Q, R, Cervid 1, and BL 25) previously described by Anderson et al. (2002), with minor modification (for detailed genetic analyses, see supplemental material, available at www.onlinelibrary.wiley.com).

We assigned parentage by year with candidate files created for potential dams, sires, and offspring based on age at time of sampling. Aging of deer ≤1.5 years is based on replacement of the third premolar (Severinghaus 1949). Aging of deer ≥2.5 years by tooth wear can be problematic, but all deer in the present study were aged using locally collected known-age deer jaws (Gee 1998, Gee et al. 2002). We assigned all deer to age classes of 0.5, 1.5, 2.5, and ≥3.5 for construction of candidate parent files and age-class breakdown of matches (DeYoung et al. 2009). We constructed candidate parent files for each year, with the age of the animals known to be alive in a given year backdated from age at harvest. For example, we considered a 2.5-year-old male harvested in 2009 to be a candidate father in the 1.5-year-old age class for offspring born in 2009 and sired in 2008. Our all-years sample breakdown among candidate fathers, for which we analyzed parentage by age class, was 28.6% yearlings, 29.6% 2.5-year-olds, and 41.8% ≥3.5-year-olds and reflected the age distribution of our collective candidate sire files. We considered males harvested in the fall of a given year to be candidate sires for the

following spring because the majority of harvest occurred during and after breeding.

We assigned parentage using Cervus v3.0 (Marshall et al. 1998, Shaw 2005). Cervus uses a maximum-likelihood method by comparing the LOD scores (a measure of how likely an individual is to be the true parent vs. not the true parent) of the 2 most likely candidate fathers to calculate a delta statistic. The critical values of the delta statistic to assign parentage at 80% and 95% confidence, respectively, were derived from parentage simulations based on population sampling parameters and allele frequencies. Because true parent–offspring pairs can contain genetic mismatches due to PCR errors, scoring error, mutation, or null alleles (Queller et al. 1993, Marshall et al. 1998, Dakin and Avise 2004, Hoffman and Amos 2005), Cervus allows for some mismatching between genotypes.

We calculated allele frequencies using our entire dataset. We ran simulations for each year, and parameters varied by year based on the estimated percentage of the population sampled by sex. We assumed a 1% typing error rate in Cervus (Sorin 2004, DeYoung et al. 2009). Following published studies, we accepted Cervus assignments at $\geq$80% confidence (Marshall et al. 1998, Slate et al. 2000, DeYoung et al. 2009).

## RESULTS

We scored an average of 716 individuals per locus (range: 708–730; Table S3). Across loci, allelic diversity ranged from 2 to 15, with a mean value 8.75/locus. Mean expected heterozygosity was 0.656 (range: 0.072–0.870), whereas mean observed heterozygosity was 0.596 (range: 0.073–0.862). Combined non-exclusion probability (i.e., the probability that a non-parent is considered as a candidate parent) across all loci was 0.015. We detected significant deviations from Hardy–Weinberg equilibrium at 4 loci (Cervid 1, BL25, N and D), resulting from an excess of homozygotes likely resulting from null alleles. Population null allele frequencies estimated to range from 0.048 to 0.083, following Brookfield (1996; Table S3). Although less extreme than this study, an excess of homozygosity has been documented at these loci, to varying degrees, across other studies (see Fig. S1). Also, these 4 loci exhibited positive inbreeding co-efficients ($F_{IS}$), ranging from 0.106 (Cervid 1) to 0.193 (D). The overall inbreeding coefficient was 0.091 (SD: 0.088). STRUCTURE analysis did not identify genetic substructure within the dataset; thus, we considered samples to be part of a single panmictic population.

Across the years sampled, we considered 445 individuals to be offspring within the sample set and included them in parentage analysis. We assigned paternity to 42 males with each siring an average of 1.33 (range: 1–5) offspring, resulting in 56 assigned deer with paternity. Sires represented all age classes (Table 1), but younger deer (i.e., 1.5 and 2.5 years old) collectively were sires for 59% of cases where paternity was assigned. We detected offspring for 69 females, with an average of 1.17/dam (range: 1–3), totaling 81 deer. Although we detected siblings likely born in the same year, we were unable to confirm multiple paternity.

**Table 1.** Percent of white-tailed deer maternity and paternity assignments by age class at Chesapeake Farms, Maryland, USA, 2003–2009, under strict (95%) and relaxed (80%) confidence.

| Age of dam or sire | Dams (%)[a] | Sires (%) |
|---|---|---|
| 0.5 | 40 | |
| 1.5 | 24 | 23 |
| 2.5 | 13 | 36 |
| 3.5+ | 24 | 41 |
| Total (no.) | 68 | 56 |

[a] An additional 13 maternal matches were assigned but not included in age analysis because age at mating was unclear.

## DISCUSSION

Our results indicate males of all age classes breed under restricted harvest. This may be contrary to what one might expect under a system that includes high numbers of older-age-class males typically associated with mating success (Hirth 1977, Marchinton and Hirth 1984). Additionally, our results are strengthened by those of genetic studies of non-QDM populations where breeding is distributed among all age classes (Sorin 2004, DeYoung et al. 2009). Although the $\geq$3.5 age class is responsible for more breeding (i.e., 41%) than any other age class at Chesapeake Farms, the 1.5- and 2.5-year-old age classes together comprise more than half (i.e., 23% and 36%, respectively) of parentage assignments. Breeding by the youngest sexually mature males (i.e., the 1.5-year-old age class) in our population is particularly interesting because of the abundance of males $\geq$3.5 years old, which are estimated to comprise more than half the male population at Chesapeake Farms (M. C. Conner, unpublished data). However, the balanced sex ratio of Chesapeake Farms could facilitate greater-than-expected breeding by subordinate males through several possible mechanisms. Most females at Chesapeake Farms are bred within a single initial rut, followed by a small secondary rut, restricting opportunities for any one male to mate with multiple females (Miller et al. 1995). Additionally, males of any age occupied by a tending bond are unable to monopolize other females, allowing competing males the opportunity to mate regardless of their dominance status (Hirth 1977, Jones et al. 2011). Observational research suggests that when older males are occupied, either by a tending bond or aggressive interactions with other males, yearling males engage in mating behaviors (Hirth 1977). Finally, the abundance of older adult males may shift interactions within that age class. Typically, dominant males establish their position ahead of the rut, but dominance may not be stable throughout the season (Hirth 1977, DeYoung et al. 2006). An abundance of physically mature males may mean dominance is less clearly defined as breeding begins because of increased competition (Hirth 1977, Ozoga and Verme 1985).

Surreptitious mating elevating the reproductive success of younger-age-class males (the 1.5-year-old age class in particular) clearly is a different strategy than that used by dominant males. Studies in other species suggest a variety of strategies (e.g., defense of territory polygyny, female choice, surreptitious mating, promiscuity) can lead to breeding

success, based on factors such as intraspecific competition, age, and social and environmental predictors (Thirgood 1991, Shuster and Wade 1991, Coltman et al. 1999, Gemmell et al. 2001). In populations where the oldest age class is relatively small, reason would suggest there is little barrier to breeding by younger males because of reduced intraspecific competition (Hirth 1977, Ozoga and Verme 1985). However, the abundance of younger males breeding at Chesapeake Farms raises the question of why the oldest age class, present in significant numbers, is unable to dominate breeding. There may be little selective benefit to monopolizing breeding among deer, considering that the spatial distribution of females and the effort required to protect them from other males mean considerable energy must be expended to find, court, and defend large numbers of females, particularly in a short time span (DeYoung et al. 2009).

Our study achieved a relatively low level of parentage assignment. Levels of parentage assignment are limited in genetic studies that use harvested animals because once an animal is sampled it is removed from the population and no longer contributing to future generations (DeYoung et al. 2009). Working with harvested deer in a QDM population further limits the number of males sampled because harvest of males is restricted. Also, our low level of paternity assignment may be partly explained by the movement dynamics of white-tailed deer from Chesapeake Farms. Karns et al. (2011) determined that 63% of collared males from Chesapeake Farms made one or more excursions outside their home range prior to or during breeding season, and the study concluded breeding factors were the likely motivators for the movements. Kolodzinski et al. (2010) determined that 90% of female white-tailed deer made excursions outside their home ranges at 2 mid-Atlantic sites, one of which was Chesapeake Farms, and the excursions appeared to occur around the time of conception, suggesting females might be actively searching for mates. The balanced sex ratio at Chesapeake Farms could motivate females to actively search for mates if the majority of males are occupied by tending bonds at any one time (Kolodzinski et al. 2010). Movements outside of home ranges and potentially beyond or onto the Chesapeake Farms property during breeding suggest a wide geographic region must be sampled to capture a reasonable percentage of sires in a given population. Because we assigned a low level of parentage, it is possible that if polyandry is present at low levels in this population, our analysis did not capture it. However, under restrained male harvest, polyandry may be minimal because the tending bond likely limits the total number of females with which any single male can mate (Hirth 1977).

Microsatellite DNA loci are widely recognized for their application in addressing questions at the individual and the population level (Avise 2004). However, analysis and the interpretation of results may be complicated by loci that deviate significantly from Hardy–Weinberg equilibrium. With an excess of homozygotes, potential factors contributing to such deviations include cryptic population substructure (Wahlund effect), genotyping or PCR errors (e.g., null

alleles), and inbreeding (Avise 2004, Dakin and Avise 2004). Our relatively low number of unscored individuals at problematic loci leads us to believe that if null alleles are present within the population screened, bias introduced for parentage analysis was minimal (Dakin and Avise 2004). The most likely outcome of null alleles in analysis involves false exclusion of the true parent (Dakin and Avise 2004), leading to lower levels of parentage assignment. Although lower levels of parentage assignment would decrease estimates of individual mating success, overall estimates of relative mating success should be unaffected as long as there is no bias associated with age.

An alternative and more plausible explanation for the excess of homozygosity observed in this study is the possibility of elevated levels of inbreeding. Here, the inbreeding coefficient deviated significantly from zero ($F_{IS} = 0.091$, 95% CI = 0.085–0.097). With 59% of paternities being assigned to younger deer (1.5-yr and 2.5-yr age classes), the likelihood of intergenerational matings is elevated. This, in turn, increases the probability of common descent in the offspring, which will result in an excess of homozygosity and elevated $F_{IS}$ (Giesel 1971).

Under QDM, fewer available females, higher competition for those females, and a trend toward lower male dispersal probability documented at Chesapeake Farms by Shaw et al. (2006) may contribute to males mating with more closely related females. Thus, a consequence of QDM, albeit unintended, may be higher levels of inbreeding. Indeed, the high proportion of paternities assigned to younger males in this study is almost double that reported by DeYoung et al. (2009) in populations in southern Texas and south-central Oklahoma, where $F_{IS}$ values ranged from 0.042 to 0.059. Further examination of genomic heterogeneity within this and other populations may shed light on this possibility.

## MANAGEMENT IMPLICATIONS

Management strategies that restrict harvest of young males may be employed, in part, to maximize the contribution of large, dominant males to the next generation, but such goals assume those males monopolize mating and survive well into adulthood. Our study suggests mating under restricted harvest of young males, a key tenet of QDM, is more balanced across age classes, and dominant males do not monopolize breeding. However, the premise of dominant males monopolizing the breeding is a common misconception, so biologists and managers need to be explicit when teaching deer hunters about expectations under QDM-style management strategies. If young males are present, they will and do contribute to breeding, but this is not inherently problematic. The phenotype of younger males is not yet fully expressed, but these future mature males are already passing their genes onto the next generation and if provided an opportunity to reach adulthood may become the dominant males in the population. Hence, QDM provides a framework for balancing the age structure of a deer population while increasing the chance that some males reach maximum phenotypic potential. Management strategies that seek to manipulate breeding by propagating the genes of dominant

males should account for the interplay among sex ratio, age structure and dominance relationships in mating success. However, managers should recognize that breeding systems are complicated and plastic, and manipulating breeding systems through factors such as sex ratio and age structure may not yield the desired result. Our results indicate the interaction between the sex ratio and age structure, fostered by strategies that balance the sex ratio and extend the male age structure, facilitate breeding by younger males. These results indicate management strategies that employ QDM-type practices with a goal of propagating the genes of dominant males may fall short, and the interplay among sex ratio, age structure, and dominance relationships may be the main influences of mating success.

## ACKNOWLEDGMENTS

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