

ABSTRACT

SHAW, JONATHAN CHRISTOPHER. Implications of quality deer management on population demographics, social pressures, dispersal ecology, and the genetic mating system of white-tailed deer at Chesapeake Farms, Maryland. (Under the direction of Dr. Richard A. Lancia)

Quality deer management (QDM) is widely accepted as a principled management practice for white-tailed deer (*Odocoileus virginianus*), yet QDM implications for population processes are unclear. Our research primarily focused on components of (1) dispersal ecology and (2) the genetic mating system of white-tailed deer under QDM at Chesapeake Farms, Maryland.

Dispersal of yearling male white-tailed deer can have profound effects on population demographics, and adversely impact population estimates and management objectives. The relationship among population demographics, social pressures, and dispersal ecology is not clear and warrants scientific evaluation of these population processes. The age structure and sex ratio of the white-tailed deer population at Chesapeake Farms, Maryland changed after implementation of QDM. Following Rosenberry's (1997) pre-QDM study on white-tailed deer dispersal we conducted a post-QDM study on white-tailed deer dispersal at Chesapeake Farms. The objectives of our dispersal ecology research were: (1) to compare pre- and post-QDM emigration, immigration, survival, and behaviors of yearling males at Chesapeake Farms, and (2) evaluate inbreeding avoidance and sexual-competition hypotheses as mechanisms of dispersal. Emigration probability of yearling males 8-18 months of age pre-QDM was 0.70 ± 0.07 , and post-QDM was 0.54 ± 0.10 ($Z = 1.39$, $P = 0.165$). Survival probability of yearling males 8-18 months of age increased from 0.44 ± 0.07 pre-QDM to 0.72 ± 0.08 post-QDM ($Z = 2.82$, $P = 0.005$) and was attributed largely to increased survival of emigrant males post-QDM. Dispersers exhibited breeding competition with other

yearling males more often than nondispersers in both pre- ($t_{19} = 3.22, P = 0.005$) and post-QDM ($t_{13} = 3.54, P = 0.004$) populations. Breeding behaviors of yearling males decreased from pre- to post-QDM ($t_{34} = 2.00, P = 0.053$). Antler points of nondisperser yearlings also decreased from pre- to post-QDM ($t_{16} = 3.29, P = 0.005$). DNA maternity analysis indicated that dispersal of orphans (4 of 7) and non-orphans (7 of 10) was similar ($X_1^2 = 0.298, P = 0.585$). Our results fail to support inbreeding avoidance and support sexual-competition as a cause of fall dispersal at Chesapeake Farms. Through QDM, an older male age structure may have suppressed breeding competition in yearling males and decreased dispersal rates, increasing site-specific management efficiency.

Investigation of white-tailed deer mating systems was previously restricted to observation of courting behaviors in enclosed populations, and inferences made on dominance rank and breeding success. The prevailing observation-based white-tailed deer mating system paradigm entails establishment of male dominance hierarchies, where few dominant males locate, guard, and breed virtually all estrous females. Advances in molecular techniques allow objective investigation of wildlife mating systems where research indicates observed social mating systems often differ from actual genetic mating systems. The objectives of our genetic mating system research were to evaluate: (1) age-specific male breeding success; (2) relationships of weight and antler size with breeding success of males ≥ 2.5 -years old; (3) instances of multiple paternity in single litters; and (4) male and female mate selection. Using microsatellite markers to assign paternity, we observed higher breeding success of males ≥ 3.5 -years old in comparison to males ≤ 2.5 -years old, indicating a breeding hierarchy existed. However, several males across age-classes bred; antler and body size were not important factors in breeding success of males ≥ 2.5 -years old; and instances of multiple paternity of single litters occurred. Our results

fail to support the prevailing observation-based mating system paradigm where few dominant males monopolize tending bonds with females, and are consistent with genetic paternity results in enclosed, mature age-structured, white-tailed deer populations. Results indicate limits to the number of estrous females a single-dominant male can locate, guard, and breed. In populations with high estrous synchrony, dominant males fail to effectively monopolize tending bonds, and subordinate males may successfully breed surplus estrous females via surreptitious fertilization.

**IMPLICATIONS OF QUALITY DEER MANAGEMENT ON POPULATION
DEMOGRAPHICS, SOCIAL PRESSURES, DISPERSAL ECOLOGY, AND THE
GENETIC MATING SYSTEM OF WHITE-TAILED DEER AT CHESAPEAKE
FARMS, MARYLAND**

by

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BIOGRAPHY

Jonathan C. Shaw was raised in a small farming community in Onslow County, North Carolina, where he graduated from Richlands High School in June of 1996. He received his Bachelor of Science Degree in Fisheries and Wildlife Science at North Carolina State University in the spring of 2000, and began his graduate research at North Carolina State University in the fall of 2000.

In addition to dispersal ecology and genetic mating system research, Jonathan was involved in adult male and female GPS collar research, and parturition habitat research for white-tailed deer at Chesapeake Farms, MD. He spent 22 months researching, and over 600 hrs observing white-tailed deer at Chesapeake Farms, MD from 2001-2004. Jonathan gained wildlife management experience as a summer employee at Chesapeake Farms, MD in 2000, a wildlife surveyor in Raleigh, NC in 1999, and wildlife laborer at Camp Lejeune, NC in 1997 and 1998. He currently resides in Raleigh, NC where he is seeking employment in wildlife management and research in North Carolina.

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INTRODUCTION TO THE DISSERTATION

The recovery of white-tailed deer (*Odocoileus virginianus*) in the southeastern United States from near extirpation in the early 20th century is likely the most successful conservation endeavor for a large mammal species (Blackard 1971, DeYoung et al. 2003). Conversely, successful white-tailed deer management in the 21st century will be dependent on control of populations that are considered overabundant in many areas (McShea et al. 1997). Ample deer harvest is a crucial component of maintaining sustainable populations below cultural and natural carrying capacities of the environment (Marchinton et al. 1990). In addition to being a highly selective browser, a single deer consumes approximately 2.5 kg of biomass daily. Consequently, high-density populations have the capacity to alter forest composition and degrade habitat quality (Augustine and DeCalesta 2003, Horsley et al. 2003, Furedi and McGraw 2004). Therefore research that evaluates current deer management practices is critical not only for deer herds, but for all forest wildlife. Research that increases understanding of the implications of prescribed management practices increases management competency, and establishes credibility with both the nonhunting and hunting public, which are invaluable tools for white-tailed deer management.

Quality Deer Management (QDM) is a widely accepted method for managing white-tailed deer in numerous areas of the United States (Hamilton et al. 1988). As stated by Joe Hamilton, founder of the Quality Deer Management Association, “Quality Management is the use of restraint in harvesting (young) bucks, combined with an adequate harvest of antlerless deer to maintain a healthy population that is in balance with the existing habitat conditions. This level of deer management involves the production of

quality deer – bucks, does, and fawns, quality habitat, quality deer hunting, and quality hunters.” Quality is a subjective term, but typically relates to vigorous and sustainable herds that comply with inherent population processes, habitat that promotes biodiversity and natural ecological processes, and safe and ethical hunters and hunting experiences. Quality deer management promotes sustainable use of deer populations by uniting landowners, hunters, and managers in a common goal of producing biologically and socially balanced deer herds within existing environmental, social, and legal constraints (Miller and Marchinton 1995).

The success of a QDM program is measured by increased health of the deer herd and habitat within the management area (Marchinton et al. 1990). To accomplish this objective, QDM promotes 3 main concepts (Miller and Marchinton 1995). First, habitat is improved through enhancement of native vegetation via sound silvicultural practices (prescribed burning, thinning, clear-cutting, reseeding, etc.), and through food plot implementation. Habitat and herd health is typically increased through ample harvest of females, which in turn improves sex ratio balance, and effectively decreases deer densities. Herd quality is enhanced through restrictive harvest of young males, which in turn further balances the sex ratio of the population, and increases the number of mature males in the population. A balanced sex ratio and older male age structure decreases rut duration. Females in a successful QDM program are bred during a brief window during the fall, and fawns are born under optimal conditions in the early spring when vegetation is succulent, and forage nutrition for lactating females, developing fetuses and fawns, and antler and body growth of males is high. A balanced sex ratio and older male age

structure also increases breeding competition in males, which could increase genetic quality.

Habitat enhancement and decreased deer densities increase available per capita deer nutrition. Improved balance in adult sex ratios, and older male age-structures increase breeding competition and promote favorable parturition timing. These management concepts intuitively should increase quality deer herds and quality wildlife habitat, yet there is a great deal of variability in the success rates of QDM programs. This variability is likely attributed to the degree of hunter/manager commitment to prescribed management practices, and deer movements across management areas with differential harvest pressures and management practices.

Hunter/manager commitment is influenced by hunter education, and the degree to which hunters/managers accept the credibility of the biologist that proposes QDM management practices. Most hunters initially accept the idea of ample doe harvest to decrease deer densities and improve sex ratios. However, hunter education is often lacking on the biological importance of these prescribed harvest strategies. Hunters often panic when densities are effectively decreased, and fewer deer are seen. Additionally, recruitment stimulation through decreased herd densities is not apparent to many hunters, hence fewer does intuitively means fewer buck fawns. Consequently, doe harvest is subsequently relaxed, and populations rebound to densities near pre-QDM implementation. Likewise restricted harvest of young males is intuitively a straightforward concept for hunters. Strict “shoot-don’t shoot” harvest regimes based on minimum antler size criteria are easy for hunters to follow, and are typically

implemented. However, these antler restriction criteria may not sufficiently protect young large-antlered males, and full QDM potential is never reached.

Hunters are more likely to conform to management practices prescribed by credible biologists. White-tailed deer research is extensive; however, the impacts of management practices akin to QDM on population processes are unclear. Research through adaptive resource management that improves understanding of these processes adds credibility to biologists while providing scientific evaluations for prescribed management practices.

Deer movements across management area boundaries with differential harvest pressures may also limit QDM success. Most deer management areas comprise of relatively small parcels (<200 ha) of privately owned land (McCoy et al. 2005). Understanding the movement patterns of deer, especially bucks, on those properties is critical for establishing and evaluating a successful QDM program. Small management areas may be limited by deer home-range movements (McCoy et al. 2005). Deer home ranges commonly exceed 200 hectares (Marchinton and Hirth 1984); therefore, few deer if any reside within the boundaries of these properties. Objectives to decrease deer densities and improve sex ratios through ample doe harvest, improve male age-structures through restricted harvest of young males, and improve habitat may be hindered by opposing management objectives on neighboring properties.

Relatively large management areas (<25,000 ha) may be less affected by home range movements, but are equally susceptible to the impacts of dispersal and differential harvest pressures across properties (Rosenberry et al. 1999, McCoy et al. 2005). Yearling male dispersal impedes site-specific management goals by impacting deer

densities, age structures, and sex ratios, therefore requiring close cooperation between management areas to reduce the effects of differential dispersal where immigration and emigration are not equal. Increased knowledge of dispersal ecology of deer can help managers assess the spatial scale at which QDM is applicable, and assess management strategies to decrease dispersal rates.

Chesapeake Farms is undoubtedly a QDM success story, where the number of mature males in the population was increased, and balance in the adult sex ratio was improved in a relatively short amount of time. The primary objective of our research was to evaluate the implications of QDM on white-tailed deer population processes at Chesapeake Farms, Maryland by (1) assessing the relationship among population demographics, social pressures, and dispersal ecology, and (2) investigating the genetic mating system.

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CHAPTER 1

Effect of population demographics and social pressures on white-tailed deer dispersal ecology

INTRODUCTION

Dispersal of white-tailed deer can have significant impacts on population demographics, which can reduce accuracy in demographic estimates and pose limits to management decisions aimed to manipulate densities, sex ratios, and age structures (Marchinton 1982). Management decisions and evaluations are dependent on accurate population demographic estimates of density, age-structures, sex ratios, survival, emigration, and immigration; however, empirical data assessing the relationship among population demographics, social pressures, and dispersal ecology are lacking. Dispersal in white-tailed deer occurs predominantly among yearling males and usually comprises >50 % of these individuals (Hawkins et al. 1971, Downing and McGinnes 1976, Kammermeyer and Marchinton 1976, Nixon et al. 1991, Nelson 1993, Demarais et al. 2000), yielding substantial exchange of individuals in the cohort (Rosenberry et al. 1999). Emigration and immigration are difficult to measure and typically assumed constant and equal in population analysis (Johnson 1994). However, when emigration and immigration are dynamic and not equal, decreased accuracy in projected population density, sex ratio, and age structure estimates occurs (Rosenberry et al. 1999).

In addition to emigration and immigration rates, associated dispersal parameters of spatial scale, timing (Brinkman et al. 2005), and survival of yearling male dispersers and nondispersers are important when forming and evaluating management decisions (Rosenberry et al. 1999). Dispersal distances are typically less than 12 km but may

exceed 200 km; therefore, the scale of demographic effects is potentially large (Sparrowe and Springer 1970, Dusek et al. 1989, Nelson 1993, Rosenberry et al. 1999, Brinkman et al. 2005). Yearling male dispersal in some populations occurs predominately in the spring fawning season around 12 months of age (Woodson et al. 1980, Nixon et al. 1991, Nixon et al. 1994, Brinkman et al. 2005) but more commonly occurs in the fall breeding season around 18 months of age (Hawkins et al. 1971, Roseberry and Klimstra 1974, Tierson et al. 1985, Nelson and Mech 1987, Dusek et al. 1989, Kilgo et al. 1996). Yearling males that disperse during the fall may be vulnerable to harvest. Consequently hunter success rates may be impacted, and management goals may be affected (McCoy et al. 2005).

High emigration rates and low survival of waiting immigrants may result in a net loss of yearling males (Rosenberry et al. 1999), warranting clarification of the cause of dispersal, and how changes in harvest strategies and population demographics influence dispersal rates. Quality deer management is widely accepted as a sound management practice for white-tailed deer and is based on manipulation of population demographics through harvest (Hamilton et al. 1988). Quality deer management aims to improve nutrition, decrease deer densities, promote mature male age-structures, and increase male to female ratios (Brothers and Ray 1975) prompting potential changes in social pressures and behaviors (Nelson and Mech 1981, Ozoga and Verme 1982, Ozoga et al. 1982, Tierson et al. 1985, Marchinton et al. 1990, Nixon et al. 1991).). Inbreeding avoidance and sexual-competition are hypothesized as ultimate mechanisms of dispersal and are connected to proximate mechanisms of dispersal; maternal/adult female aggression towards yearling males (Ozoga and Verme 1985, Holzenbein and Marchinton 1992*a*,

Nixon et al. 1994) and male breeding competition (Kammermeyer and Marchinton 1976, Marchinton 1982, Marchinton and Hirth 1984, Rosenberry et al. 2001), respectively. If social pressures are the cause of dispersal then changes in population demographics prompted by QDM may impact dispersal rates.

Despite copious research on the dispersal of white-tailed deer (Hawkins et al. 1971, Downing and McGinnes 1976, Kammermeyer and Marchinton 1976, Dusek et al. 1989, Nelson 1993, Brinkman et al. 2005), evaluation of proximate mechanisms and the connections among population demographics, social pressures, and dispersal ecology have received little attention. Results of yearling male orphan studies to evaluate the maternal aggression hypothesis are inconsistent, suggesting maternal aggression may be a viable cause of dispersal in some populations (Holzenbein and Marchinton 1992*a*), but not in others (Woodson et al. 1980, Nixon et al. 1994). Behavioral data have been used to make inferences about proximate mechanisms prompting dispersal (Ozoga and Verme 1985, Holzenbein 1990); however, quantitative behavioral comparisons of dispersers and nondispersers and simultaneous tests of both inbreeding avoidance and sexual-competition hypotheses are limited (Rosenberry et al. 2001). Estimates of immigration are difficult to obtain and often ignored (Rosenberry et al. 1999) whereas estimates of differential dispersal of emigrants and immigrants (Marchinton 1982) are needed to more accurately evaluate population processes. In addition, assertions that management strategies aimed to increase male to female ratios and increase male age-structures reduce dispersal rates by decreasing maternal/adult female aggression towards yearling males (Marchinton et al. 1990) or suppressing yearling male breeding competition (Rosenberry 1997) have not been quantified.

The objectives of our study were: (1) to evaluate the impacts of population demographics on emigration, immigration, survival, and behaviors of yearling males by comparing pre- and post-QDM estimates of these parameters at Chesapeake Farms; (2) to evaluate inbreeding avoidance and sexual competition hypotheses as mechanisms of dispersal through behavioral comparisons of dispersers and nondispersers; and (3) to evaluate the maternal aggression hypothesis by comparing dispersal rates of orphan and nonorphan yearling males determined by genetic maternity analysis.

STUDY AREA

We conducted fieldwork from January 2001 to December 2002 at Chesapeake Farms (formerly Remington Farms), a 1,330 ha wildlife management and agricultural research and demonstration area operated by DuPont Crop Protection. Chesapeake Farms is located on the eastern shore of the Chesapeake Bay in Kent County, Maryland, 10 km southwest of Chestertown. The study area was approximately 50% forested with non-alluvial swamps that consisted predominately of oaks (*Quercus palustris*, *Q. alba*, *Q. phellos*, and *Q. rubra*.), sweetgum (*Liquidambar styraciflua*), black gum (*Nyssa sylvatica*), and red maple (*Acer rubrum*) with understory of greenbrier (*Smilax* spp.), sweet pepperbush (*Clethra alnifolia*), and highbush blueberry (*Vaccinium corymbosum*). Twenty percent of the study area consisted of crop fields with soybeans, corn, and winter wheat. Thirteen percent of the area consisted of fallow fields with a mix of orchard grass, clover, rye, and sunflowers. The remaining 17% of the area consisted of multiflora rose (*Rosa multiflora*) and other early successional species along with 80 ha of man-made waterfowl impoundments (Rosenberry 1997).

Harvest occurred primarily during a 1-week (1988-1992) and 2-week shotgun season (1993-2002) in late November and early December, with limited harvest during primitive-weapons seasons from mid-September through late January. Selective male harvest based on antler criteria was initiated in 1994 (<7 points restricted harvest) and modified in 1997 (<40 cm outside spread restricted harvest). We refer to the 1994 - 1996 populations at Chesapeake Farms during fieldwork conducted by Rosenberry (1997), Rosenberry et al. (1999), and Rosenberry et al. (2001), and the 2001 - 2002 populations at Chesapeake Farms during our fieldwork as pre- and post-QDM populations, respectively.

METHODS

Post-QDM methods generally parallel pre-QDM methods described by Rosenberry (1997), and Rosenberry et al. (1999), (2001) with exceptions noted. Results are presented with SE and 2-tailed *P*-values.

Population Demographics

From 1988–2002, researchers collected data from deer harvested at Chesapeake Farms, and estimated ages from tooth wear and replacement (Severinghaus 1949), where lower mandibles were compared to known-aged deer mandibles at Chesapeake Farms. Additionally, 1988–2002, Chesapeake Farms guest hunters completed field surveys that included query of the number of hours hunted, and number of antlered and antlerless deer seen. We compared 1994-1996 and 2000-2002 mean yearly harvest of males ≥ 3.5 years of age, and the mean yearly proportion of antlered deer observed by Chesapeake Farms guest hunters on the first 2-days of Maryland’s shotgun season with two-sample *t* tests.

Natal Dispersal and Survival

Field Techniques.--We captured deer from January to April 2001 and 2002 with a drop-net (Conner et al. 1987, Lopez et al. 1998). After net capture, we blindfolded and sedated deer with an intramuscular dose of approximately 0.5 mg/kg of xylazine in 2001, and increased dosage to 2.0 mg/kg in 2002 to reduce capture induced mortality. Prior to release, each deer received an intramuscular dose of approximately 0.2 mg/kg yohimbine (Wallingford et al. 1996). All deer received numbered monel and livestock ear tags. Dispersal typically occurs ≥ 11 months of age (Nixon and Etter 2001); therefore, male fawns captured at 7-10 months of age were assumed nonimmigrants and received solar-powered ear tag radio transmitters with mortality sensors (ATS, Asanti, MN 55040) (Rosenberry et al. 1999).

We determined natal dispersal and survival by locating radio-tagged deer 2-3 times/week from a truck-mounted null-peak system with a $\pm 5^\circ$ accuracy. A single observer located animals by taking two or more azimuths within 20 minutes of each other from differentially corrected Global Positioning System receiver locations (Rosenberry et al. 1999). Locations were calculated in Locate II (Nams 2001) and plotted in Arcview 3.3 (ESRI, Redlands, CA). We increased monitoring to 5-6 times/week during high dispersal periods (May-June and September-November), and used vehicle or aircraft to locate animals that dispersed off Chesapeake Farms every 7 to 10 days.

Data Analysis.--We defined dispersal as the permanent movement of at least one natal range diameter from the center of a yearling male's natal range (Rosenberry et al. 1999). We determined natal ranges using a minimum of 10 locations per individual to construct Mohr's Minimum convex polygons (Mohr and Stumpf 1966). The mean of

north-south and east-west coordinates of locations between 7 and 10 months of age defined natal range center of activity. The longest distance along either the north-south or east-west axis of the natal range defined natal range diameter (Rosenberry et al. 1999).

We used a staggered entry Kaplan-Meier procedure (Pollock et al. 1989) that allowed for animals to be right censored to estimate survival probabilities and emigration probabilities (1-Survival) for males 8-18 months of age (Rosenberry et al. 1999).

Additionally a Z-statistic was used to compare survival of dispersers and nondispersers and emigration rates pre- and post-QDM (Pollock et al. 1989). Based on peak neonate captures ($n = 183$) at Chesapeake Farms, we assumed a birth date of 1 June.

Emigration and Immigration

Field Techniques--A single observer estimated pre- and post-fall dispersal populations of yearling males with a mark-resight method by recording individual antler configuration and body characteristics of yearling males with a 15-60X spotting scope from 4.5-m-high stands. Observation of an individual for 2 or more minutes defined a marking event (Rosenberry et al. 1999). Mark-resight periods occurred for a 4-week period in August and a 3-week period in November for pre- and post-dispersal estimates, respectively. Sampling occurred in places where deer were highly visible. A sampling period consisted of a 5-day-week of sampling from 5 observation stands for approximately 2.5 hrs each evening.

In each of the 5 observation areas, we placed an infrared-triggered camera (Non Typical, Inc.) in high deer traffic areas to increase capture probabilities (Rosenberry et al. (1999) did not use infrared-triggered cameras). We used salt blocks and shelled corn to lure deer to cameras pre- and post-dispersal, respectively. A photograph that revealed

distinguishable antler characteristics of an individual defined a marking event. We censored individuals that could not be positively identified. Photograph marking sessions coincided with observation marking sessions. Additionally, we concentrated observation stands and cameras in a 400 ha area of Chesapeake Farms to increase capture probabilities within the marking area. Individuals observed or photographed in multiple observation areas were counted only once per weekly marking session.

Data Analysis.-- Closure was assumed for pre- and post-fall dispersal population estimates because our marking periods were relatively short (≤ 4 weeks), and they occurred during periods of high yearling male survival at Chesapeake Farms (Rosenberry et al. 1999). Capture probabilities influenced by heterogeneity, time, and behavioral responses were addressed by using program CAPTURE (Otis et al. 1978, Pollock et al. 1990) to select the appropriate model for population estimates. A single investigator observed yearling males for approximately 2.5 hrs a day, 5 days a week, from early May to late November. Therefore, familiarity with individual deer was high during marking periods (August and November), decreasing the likelihood that individuals were misidentified.

We estimated the number of emigrants as the product of the pre-dispersal population and the probability of emigration.

$$Emigrants = \hat{N}_{pre-dispersal} * P_{emigrating}.$$

$$Var(Emigrants) = 2\hat{N}_{pre-dispersal} * var(P_{emigrating}) + 2P_{emigrating} * var(\hat{N}_{pre-dispersal}) + var(\hat{N}_{pre-dispersal}) * var(P_{emigrating}).$$

We estimated the number of immigrants as the post-dispersal population minus the product of the pre-dispersal population and the probability of a yearling male surviving and not emigrating. (Rosenberry et al. 1999).

$$\begin{aligned}
 \text{Immigrants} &= \hat{N}_{\text{post-dispersal}} - \hat{N}_{\text{pre-dispersal}} * P_{\text{surviving and not emigrating}}. \\
 \text{Var(Immigrants)} &= \text{var}(\hat{N}_{\text{post-dispersal}}) + 2\hat{N}_{\text{pre-dispersal}} * \text{var}(P_{\text{surviving and not emigrating}}) + \\
 &2P_{\text{surviving and not emigrating}} * \text{var}(\hat{N}_{\text{pre-dispersal}}) + \text{var}(\hat{N}_{\text{pre-dispersal}}) * \text{var}(P_{\text{surviving}} \\
 &\text{and not emigrating}).
 \end{aligned}$$

The difference in the number of immigrants and emigrants (immigrants – emigrants) each year defined differential dispersal. We used a Z-statistic to compare pre- and post-QDM differential dispersal.

Observations

Field Techniques.--Social interactions were observed with a 15-60X spotting scope from 4.5-m-high observation stands during the breeding season. Breeding season was defined by the onset of sparring, through the end of fall dispersal (mid August – mid November, 2001, 2002) (Rosenberry et al. 2001). A single observer made observations primarily during mornings and evenings when deer were most active (Kammermeyer and Marchinton 1977) and 5 or more times a week for approximately 2.5 hrs per observation session.

We defined and recorded behaviors (Thomas et al. 1965, Hirth 1977) between radio-marked yearling males and other individuals of determined age and sex. The presence or absence of antlers defined sex of deer ≥ 1 year of age. Age was recorded as fawn (<12 months), yearling (12-24 months of age), or adult (>24 months of age) based

on age-related morphological characteristics, antler size, and facial conformation. We timed observation sessions, and recorded interactions as a rate (interactions/hr) (Rosenberry et al. 2001).

Data Analysis.--We censored yearling males observed <15 minutes to avoid potential outliers (e.g., a yearling male with 2 interactions in 10 minutes total observation would yield an abnormal interaction rate of 12.00 interactions/hr). We analyzed nonbreeding agonistic (e.g., hard look – ear drop, strike) and breeding behaviors (e.g., present threat, sparring) separately (Koutnik 1981, Rosenberry et al. 2001), and analyzed differences in interaction rates of dispersers and nondispersers, and pre- and post-QDM interaction rates with two-sample *t* tests. We used Welch's approximate *t* test when sample variances varied greatly ($P < 0.05$) (Zar 1999).

Maternity Genetics

Field techniques.--From September 2000 – July 2004 we collected ear or tongue tissue from captured ($n = 122$) and harvested ($n = 621$) deer at Chesapeake Farms. We isolated tissue samples with Qiagen® mini-spin columns following the recommended supplier protocol (DNeasy™ Tissue Kit; QIAGEN Genomics Inc.). Fifteen microsatellite markers (BM4208, BM6438, BM6506, BM848, Cervid 1, D, ETH152, ILSTS011, INRA011, N, O, OarFCB193, OCAM, P, and Q) were selected based on marker performances outlined in Anderson et al. (2002).

Single polymerase chain reactions (PCR) amplified fluorescent-tagged primers with a PE Gene Amp® 9600 thermocycler (Applied Biosystems Inc.). Mixtures for PCR amplification contained 5.00 µl Qiagen® HotStarTaq® Master Mix, 0.20 µl of 10 µM forward and reverse primers each, and 4.60 µl of 20 ng/µl DNA and H₂O, per reaction.

Amplification conditions consisted of 15 min at 95 °C denaturation, 40 cycles of PCR, 50 sec at 95 °C denaturation, 50 sec at 60 °C annealing, 1 min 25 sec at 72 °C extension, 30 min at 72 °C extension, and held indefinitely at 4 °C. We diluted PCR products (1:60) with H₂O and pooled by a panel of 3 markers. Size standard and formamide were added to pooled samples (*rox* 500; Applied Biosystems). Pooled samples were loaded on an ABI Prism® 3700 DNA Analyzer (Applied Biosystems) for separation and detection. We analyzed DNA with GeneScan® (Applied Biosystems) and scored alleles with Genotyper® (Applied Biosystems).

Data Analysis.--We assigned maternity with CERVUS 2.0, which allowed for error rates in allele assignment by using a likelihood approach rather than an exclusion approach (Marshall et al. 1998). A log of likelihood ratio (LOD) score was generated for each possible pair of candidate dam and offspring. A *delta* score was generated as the difference in the most likely candidate dam LOD score and the second most likely candidate dam LOD score for each offspring. CERVUS 2.0 used a simulated distribution of *delta* statistics to assign a confidence level of correct maternity for the most likely candidate dam. We accepted maternity for most likely candidate dams at a $\geq 80\%$ confidence level.

Harvest of a yearling male's dam at Chesapeake Farms prior to fall dispersal defined orphan status. Known living dams during fall dispersal (dams captured or harvested after fall dispersal) defined nonorphan status of yearling males, and known harvest of dams prior to dispersal defined orphan status of yearling males. Orphan status was undetermined if maternity was assigned with $< 80\%$ confidence. We compared dispersal rates of orphans and nonorphans with a χ^2 statistic.

RESULTS

Population Demographics

Based on yearling male natal range diameters, yearling male mark/remark population estimates, and observed sex and age ratios during behavioral observation sessions, post-QDM deer density prior to hunting season was approximately 33-deer/km². In comparison, pre-QDM deer density prior to hunting season was approximately 50-deer/km² (Rosenberry 1997). Based on neonate captures ($n = 183$, 1994-2002), pre- and post-QDM peak conception and birth was similar and occurred at approximately 12 November and 1 June, respectively.

Relatively low antlerless harvest and high yearling male harvest occurred 1988-1993 (Table 1). As a result, harvest and observation data indicated a female skewed and young male age-structured population existed 1994-1996. Antlerless harvest increased, and the mean yearly proportion of antlered deer observed by hunters on the first 2 days of Maryland's shotgun season increased over time from 0.12 ± 0.02 (1994-96) to 0.18 ± 0.01 (2000-2002) ($t_4 = 3.30$, $P = 0.030$). Based on historic antler spread harvest data at Chesapeake Farms, males ≥ 3.5 years of age in the Chesapeake Farms population met the 40 cm outside antler spread harvest restriction criteria and were vulnerable to harvest (1994-1996) and (2000-2002). Similar hunter hour effort and harvest of antlered deer occurred between 1994-1996 and 2000-2002. Under similar harvest pressure, the mean yearly harvest of males ≥ 3.5 years of age increased from 7 ± 3 (1994-96) to 18 ± 2 (2000-2002) ($t_4 = 3.29$, $P = 0.030$), indicating an increase of adult males in the post-QDM population (Jenks et al. 2002).

Natal Dispersal and Survival

We caught 37 males (≤ 10 months of age) post-QDM (2001-2002) with drop-net and censored 9 due to dropped transmitter or transmitter malfunction. Yearling male natal range diameter was 0.9 ± 0.1 km estimated from 23 ± 2 locations. Median dispersal distance in both pre- and post-QDM populations was 6 km (range 2-58 km, $n = 51$, pre-QDM; range 2-16 km, $n = 16$, post-QDM). Emigration probabilities from both years post-QDM did not differ ($Z = 0.76$, $P = 0.447$) and were pooled. Post-QDM emigration probability of males 8 to 18 months was 0.54 ± 0.10 ($n = 37$). In comparison, pre-QDM emigration probability of males 8 to 18 months was 0.70 ± 0.07 ($n = 75$) (Rosenberry et al. 1999) ($Z = 1.39$, $P = 0.165$) (Table 2). In both pre- and post-QDM populations approximately 25% of emigration occurred in the spring fawning season (April-June) at 10 to 12 months of age, and 75% occurred in the fall breeding season (September-November) at 15 to 17 months of age (Figure 1).

Survival probabilities from both years post-QDM did not differ ($Z = 1.57$, $P = 0.116$) and were pooled. Causes of mortality included hunting ($n = 8$) and epizootic hemorrhagic disease ($n = 1$). We observed similar survival rates of dispersers (0.93 ± 0.06 , $n = 15$) and nondispersers (1.00 ± 0.00 , $n = 11$) at the end of fall dispersal (8-17 months of age) ($Z = 0.65$, $P = 0.516$). Overall post-QDM survival probability of males 8 to 18 months of age was 0.72 ± 0.08 ($n = 37$), whereas pre-QDM survival probability of males 8-18 months of age was 0.44 ± 0.07 ($n = 75$) (Rosenberry et al. 1999) ($Z = 2.82$, $P = 0.005$) (Table 2). The difference was largely attributed to lower survival of dispersers pre-QDM (0.62 ± 0.08 , $n = 38$) (Rosenberry et al. 1999) in comparison to dispersers post-

QDM (0.93 ± 0.06 , $n = 15$) ($Z = 3.10$, $P = 0.002$) at the end of fall dispersal (8-17 months of age).

Emigration and Immigration

Average post-QDM yearling male population was 57 ± 6 pre-dispersal and 65 ± 7 post-dispersal (CAPTURE model $M(h)$). We estimated 28 ± 5 emigrants and 37 ± 7 immigrants per year ($Z = 1.05$, $P = 0.294$). Differential fall dispersal of yearling males was $+9 \pm 9$ post-QDM. Conversely, differential fall dispersal of yearling males was -8 ± 14 pre-QDM (Rosenberry et al. 1999) ($Z = 1.06$, $P = 0.289$) (Table 2).

Observations

Post-QDM breeding season (mid August – early November) individual observation times were 1.91 ± 0.51 hr ($n = 5$) for dispersers and 1.22 ± 0.23 hr ($n = 10$) for nondispersers ($t_{13} = 1.44$, $P = 0.173$). Nonbreeding agonistic interaction rates with adult females were similar for dispersers (0.99 ± 0.27 interactions/hr) and nondispersers (1.12 ± 0.32 interactions/hr) ($t_{13} = 0.24$, $P = 0.812$), comparable to pre-QDM agonistic behavior results (Rosenberry et al. 2001) (Table 3). Collectively, disperser and nondisperser yearling male agonistic interactions with adult females were similar pre- (0.57 ± 0.27 interactions/hr) and post-QDM (1.08 ± 0.23 interactions/hr) ($t_{34} = 1.35$, $P = 0.186$) (Table 2).

Most post-QDM breeding interactions involved competition between yearling males, whereas only 6% involved breeding competition with adult males. Post-QDM dispersers were involved in breeding interactions with yearling males (2.97 ± 0.90 interaction/hr) more often than nondispersers (0.42 ± 0.26 interaction/hr) ($t_{13} = 3.54$, $P = 0.004$), comparable to pre-QDM breeding behavior results (Rosenberry et al. 2001)

(Table 3). However, collectively disperser and nondisperser yearling male breeding interactions decreased from pre- (2.58 ± 0.41 interactions/hr) to post-QDM (1.34 ± 0.45 interactions/hr) ($t_{34} = 2.00$, $P = 0.053$) (Table 2).

Comparing dispersers to nondispersers, pre-QDM dispersers tended to have fewer antler points (3.5 ± 0.4 , $n = 16$) than nondispersers (4.6 ± 0.7 , $n = 7$) ($t_{21} = 1.42$, $P = 0.169$), and dispersers tended to be more subordinate than nondispersers in breeding interactions ($X_1^2 = 2.79$, $P = 0.095$) (Rosenberry et al. 2001). In contrast to pre-QDM results, post-QDM dispersers had more antler points (4.3 ± 0.5 , $n = 15$) than nondispersers (2.5 ± 0.3 , $n = 11$) (Welch's test, $t_{22} = 3.50$, $P = 0.002$), and dispersers tended to be more dominant than nondispersers in breeding interactions ($X_1^2 = 1.32$, $P = 0.125$) (Table 3).

Maternity Genetics

Our $\geq 80\%$ confidence maternity acceptance criteria was supported by CERVUS 2.0 maternity analysis results of 8 neonates (<8 hrs of age) with known dams captured via vaginal transmitter recovery at Chesapeake Farms in 2001 (J. L. Bowman, Department of Entomology and Applied Ecology at the University of Delaware, unpublished data). CERVUS 2.0 assigned the correct most likely candidate dam for all 8 vaginal transmitter recovery neonates; 4 accepted at 80% confidence, and 4 at 95% confidence. We assigned a most likely candidate dam at $\geq 80\%$ confidence to 17 of 32 yearling males with known dispersal status. We observed similar dispersal rates of orphans (4 of 7) and nonorphans (7 of 10) ($X_1^2 = 0.298$, $P = 0.585$). Seven of 15 yearling males of undetermined orphan status also dispersed.

DISCUSSION

In both pre-QDM (Rosenberry et al. 1999) and post-QDM populations at Chesapeake Farms, dispersal occurred primarily in the fall, and dispersal distances were similar. However, our results indicate pre- and post-QDM differences in yearling male emigration, immigration, and survival. Point estimates indicated decreased dispersal, while survival of yearling males, particularly yearling male dispersers, increased from pre-QDM (Rosenberry et al. 1999) to post-QDM. Increased survival of dispersers indicates decreased harvest pressure on yearling males in adjacent management areas. Chesapeake Farms along with the Quality Deer Management Association have played an active role in educating hunters and landowners in western Kent County, Maryland in an attempt to establish QDM countywide. We believe that the well-known success of QDM on Chesapeake Farms, coupled with educational lectures given locally have played an important role in changing hunter attitudes and decreasing harvest pressure on yearling males in western Kent County, Maryland.

Although emigration and immigration were statistically similar, our estimates are plausibly representative of differential dispersal processes at Chesapeake Farms. Point estimates indicated a net loss of yearling males pre-QDM, and a net gain of yearling males post-QDM after fall dispersal. We believe this reflects higher survival of waiting immigrants, and lower dispersal rates at Chesapeake Farms post-QDM. Decreased dispersal may have occurred, indicating changes in harvest strategies and population demographics may have impacted social pressures (Ozoga et al. 1982, Tierson et al. 1985, Marchinton et al. 1990, Nixon et al. 1991) and dispersal ecology.

Post-QDM behavioral results were based on dispersers ($n = 5$) and nondispersers ($n = 10$) observed for 1.91 ± 0.52 hrs and 1.22 ± 0.23 hrs, respectively. Relatively small sample sizes may warrant reservations in behavioral result interpretation. Nonetheless, post-QDM disperser and nondisperser behavioral interaction trends were consistent with pre-QDM disperser and nondispersers behavioral interaction trends where dispersers ($n = 14$) and nondispersers ($n = 7$) were observed 1.69 ± 0.28 hrs and 1.24 ± 0.39 hrs, respectively (Rosenberry et al. 2001).

In accordance with the inbreeding avoidance hypothesis, increased aggression from adult females is related to dispersal (Ozoga and Verme 1985, Holzenbein and Marchinton 1992*b*), and increased female harvest results in decreased adult female aggression towards yearling males (Marchinton et al. 1990). In both pre-QDM (Rosenberry et al. 2001) and post-QDM populations, interactions with adult females were rare, and dispersers and nondispersers did not differ in nonbreeding agonistic interactions with adult females. Additionally, despite increased doe harvest and increased antlered to antlerless ratios post-QDM, we observed no difference in pre- and post-QDM adult female nonbreeding agonistic interactions with yearling males. Based on these results we fail to support the notion of adult female aggression as a mechanism for fall dispersal at Chesapeake Farms.

Under the maternal aggression hypothesis, the probability of dispersal is greater for nonorphans than orphans due to potential antagonism from dams immediately before and during dispersal periods. Holzenbein and Marchinton (1992*a*) determined that a significantly higher rate of emigration in nonorphans supported the maternal aggression hypothesis. However, Woodson et al. (1980) and Nixon et al. (1994) failed to detect a

difference in emigration rates of orphans and nonorphans suggesting the mechanism for dispersal might differ among populations. Likewise, we observed no difference in dispersal rates of orphans and nonorphans, failing to support the maternal aggression hypothesis. Additionally, the dispersal rate of undetermined orphans was similar to orphan and nonorphan dispersal rates at Chesapeake Farms. Undetermined orphans were not assigned a dam in our genetic parentage analysis; therefore, this group likely included a prevalence of nonorphan yearling males with dams who were not harvested and DNA not collected prior to the 2003-hunting season.

A presumption of the sexual-competition hypothesis is that increased breeding competition among males promotes dispersal (Kammermeyer and Marchinton 1976, Marchinton 1982, Marchinton and Hirth 1984, Rosenberry et al. 2001, McCoy et al. 2005) and suppression of yearling male breeding competition may decrease dispersal (Rosenberry 1997). Most dispersal in both pre-QDM (Rosenberry et al. 1999) and post-QDM populations at Chesapeake Farms occurred in the fall, coinciding with periods of high breeding competition. In both pre-QDM (Rosenberry et al. 1999) and post-QDM populations, dispersers were involved in breeding interactions earlier and more often than nondispersers, supporting the sexual-competition hypothesis as a mechanism for fall dispersal at Chesapeake Farms. Of these breeding interactions, most involved competition between yearling males.

We detected few breeding interactions between yearling and adult males pre- and post-QDM despite increased numbers of adult males post-QDM. Although statistically similar ($P = 0.053$), point estimates of yearling male breeding interactions decreased from pre- to post-QDM, which may indicate an increased number of adult males indirectly

impacted yearling male breeding interactions. Signposts are positively correlated with density of males ≥ 2.5 years old (Miller et al. 1987a), and pheromones or semiochemicals from adult males and their signposts may decrease yearling male breeding behaviours via a suppressor effect (Forand et al. 1985, Miller et al. 1987b, Marchinton et al. 1988, Marchinton et al. 1990). The suppressor effect occurs when mature males reduce the libido, competitiveness, and testosterone levels of young males (Marchinton et al. 1990). In support of the sexual-competition hypothesis, point estimates suggest decreased yearling male breeding competition and consequently decreased dispersal from pre- to post-QDM.

These notions concur with the Dispersal Theory (Geist 1978). Maintenance phenotypes (both yearling and adult nondispersers) remained prudent, had an established social order, and did not engage in excessive levels of breeding behaviors. Dispersal phenotypes were profligate, did not conform to social order, and engaged in disproportionate levels of breeding behaviors. A limited resource (i.e. mates) was defended by the maintenance phenotype, which collectively would profit from long-term prudent behavior. Maintenance phenotypes controlled and essentially rejected profligate individuals that acted recklessly towards limited resources. When resources are limited, natural selection favors maintenance phenotypes. At Chesapeake Farms, an increased number of adult males and balanced adult sex-ratio post-QDM likely limited mate availability for males, favoring maintenance (nondispersers) phenotypes; hence, lower dispersal rates were observed post-QDM.

If sexual competition causes dispersal (Kammermeyer and Marchinton 1976, Marchinton 1982, Marchinton and Hirth 1984, Rosenberry et al. 2001, McCoy et al.

2005), and age and antler size are related to rank in the male dominance hierarchy (Townsend and Bailey 1981), then an associative relationship may exist between antler size and dispersal of yearling males (Rosenberry 1997, McCoy et al. 2005). Our data indicated a relationship existed between antler points and dispersal at Chesapeake Farms; however, the relationship was different pre- and post-QDM. Nondispersers tended to have more antler points than dispersers pre-QDM. In contrast, nondispersers had fewer antler points than dispersers post-QDM. Similarly, McCoy et al. (2005) found spike antlered yearlings were less likely to disperse than branched antlered yearlings in the mature male age-structured population at the Laureles Division of the King Ranch, Texas, USA.

We believe these relationships are explained by rank and shift in the male dominance hierarchy subsequent to QDM implementation. Young males are less aware of their rank in the dominance hierarchy than adult males, and are commonly involved in sparring activities prior to peak rut in attempt to establish rank (Marchinton and Hirth 1984). We hypothesize marginal breeders are individuals with high libidos that actively pursue a position in the dominance hierarchy through sparring and other related breeding behaviors. Marginal breeders fail to establish dominance rank and seek alternative reproductive strategies, which may include surreptitious fertilization (DeYoung et al. 2002) or dispersal in attempt to improve rank. Dispersal in turn can be advantageous by increasing breeding opportunities and reproductive fitness.

A shift in the male age structure of deer at Chesapeake Farms conceivably has resulted in a shift in the male breeding population. In a population lacking adult males, yearling males may be successful sires (Ozoga and Verme 1985). We hypothesize, pre-

QDM adult males and large-antlered yearlings were primary breeders, while small-antlered yearlings were marginal breeders and dispersed. Post-QDM, an increased number of adult males displaced large-antlered yearlings as primary breeders (Miller et al. 1995); consequently, large-antlered yearlings displaced small-antlered yearlings as marginal breeders. Post-QDM adult males were primary breeders, large-antlered yearling bucks were marginal breeders and dispersed, and small-antlered bucks, via the suppressor effect, were largely non-breeders (Marchinton et al. 1990) (Figure 2). If these notions are correct, some small-antlered/subdominant 2-year olds were marginal breeders post-QDM and may have dispersed. If discrepancies in yearling male harvest pressures existed across adjacent management areas, the relationship between antler size and dispersal confounds the issue of differential dispersal. Specifically, QDM properties that are surrounded by non-QDM properties may lose large-antlered yearlings that are not replaced from surrounding properties.

At Chesapeake Farms, Maryland, point estimates of emigration and immigration indicated net loss of yearling males pre-QDM, and a net gain of yearling males post-QDM after fall dispersal; likely the result of decreased emigration and increased survival of waiting immigrants. Our results support sexual-competition as a viable mechanism of fall dispersal at Chesapeake Farms, and we detected no evidence of inbreeding avoidance associated with maternal/adult female aggression. Yearling male breeding competition was likely suppressed by adult males post-QDM; as a result, dispersal rates may have been reduced pre- to post-QDM. We hypothesize marginal breeders disperse in the fall, whereas small-antlered and large-antlered yearlings were marginal breeders pre- and post-QDM, respectively.

White-tailed deer dispersal typically occurs in discrete periods of social changes; the spring fawning season and fall breeding season. Therefore, social pressures have received the most attention as proximate mechanisms of dispersal (Hawkins et al. 1971). The relationship among population demographics, social pressures, and dispersal ecology is complex. Dispersal is a process rather than an incident, where the mechanism is likely an accumulation of dynamic environmental, biological, genetic, and social forces (Dobson and Jones 1985). In addition to social pressures, habitat quality, herd density, genetic predisposition, and perceptual cues likely influence dispersal ecology. Plasticity is commonly observed in white-tailed deer where stimuli impact populations and individuals differently over space and time (Miller 1997). Consequently, dispersal timing and distance, emigration, immigration, and the mechanism of dispersal may vary.

MANAGEMENT IMPLICATIONS

Dispersal can potentially have adverse effects on management goals aimed to manipulate deer densities, age structures, and sex ratios, all of which may warrant reduced dispersal rates to increase management efficiency. In areas where breeding competition causes dispersal, selective male harvest may decrease dispersal by increasing the number of adult males and consequently suppressing breeding competition in yearling males. In areas where adult female aggression may cause dispersal, increased female harvest may decrease adult female aggression and consequently decrease dispersal (Marchinton et al. 1990).

Ignoring dispersal or assuming equal emigration and immigration may cause bias in population demographic estimates. Dispersal and associated parameters are likely dynamic over space and time. Ideally, estimates of these parameters should be tailored to

specific management areas. Realistic time and budget constraints are limiting factors; therefore, awareness of potential biased estimates provoked by dispersal and use of conservative estimates is necessary. A basic understanding of scale and time of dispersal is advised to form local management decisions.

Many management areas have little interior space and are not large enough to contain entire dispersal movements of yearling males (Rosenberry et al. 1999). In addition, harvest seasons often occur prior to and during dispersal periods, causing differential dispersal across management areas, and reduced site-specific management efficiency (Brinkman et al. 2005). Hence, the effects of dispersal on population demographics can be substantial for management areas and large-scale cooperatives and timely harvest regulations are needed.

At Chesapeake Farms, 52 of 54 emigrants established a new home-range outside of the 1,330 ha management area, and most dispersal occurred from mid-September to early November. However, Chesapeake Farms effectively increased the number of mature males in the population within approximately 5 years. Maryland's traditional weapon (archery, muzzleloader) season opened mid-September, however most harvest (approximately 80%) occurred during a 2-week shotgun season that opened late-November, post-fall dispersal. Limited harvest via traditional weapons prior to and during fall-dispersal likely increases survival of potential immigrants. In addition, since initial implementation of QDM at Chesapeake Farms, adjacent management areas have increasingly adopted antler restriction programs. Hence, timely harvest regulations and common management objectives with adjacent management areas can reduce adverse effects of dispersal on management goals.

Heritability of yearling male white-tailed deer antler characteristics is controversial (Brothers and Ray 1975, Kroll 1991, Brothers et al. 1995), and the degree of heritability is variable (Williams et al. 1994, Lukefahr and Jacobson 1998). However, if a relationship between yearling male antler characteristics and “genetic potential” exists, our data indicated increased numbers of adult males in the population lead to an overall reduction of dispersal, but higher dispersal rates of “quality” yearlings. An objective of QDM programs is to decrease harvest related mortality of yearling males, which increases the number of adult males in the population. Quality deer management programs ultimately aim to increase the quality of bucks, does, and fawns, improve herd health, and provide quality-hunting experiences (Hamilton et al. 1995). While increasing the male age-structure may decrease dispersal and increase harvest protection of yearling males, overall buck quality may be compromised by increased dispersal rates of “quality” yearlings. Hence the objective to increase the number of adult males in the population may oppose objectives to improve buck quality and provide quality-hunting experiences. Large-scale QDM-cooperatives provide an alternative to this potential issue where large-antlered yearling bucks lost in the dispersal process are replenished by adjacent management areas.

Regardless of the relationship between yearling male antler size and “genetic potential,” large-scale cooperatives or timely harvest regulations are needed to negate limits to management objectives posed by yearling male dispersal. Equitably low harvest pressure of yearling males across management areas prior to and during dispersal periods increases efficiency in site specific management and reduces the effects of yearling male dispersal on population demographics, and potentially genetics. Otherwise, a matrix of

differential harvest pressures of yearling males across management areas prior to and during dispersal leads to management regimes where efficiency is dependent on management practices of adjacent areas.

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Table 1. Mean yearly harvest of antlerless and antlered (by age in years) white-tailed deer and proportion of antlered deer observed at Chesapeake Farms, Maryland (1988-2002) presented in 3-year increments. Harvest occurred primarily during a 1-week shotgun season (1988-1992) and 2-week shotgun season (1993-2002) in late November and early December, with limited harvest during primitive-weapons seasons during early fall and late winter.

Years	<u>Antlerless harvest</u>				<u>Antlered harvest</u>							
	Female	SE	^a MF	SE	1.5	SE	3	SE	≥ 3.5	SE	[*] Antlered	SE
^b 1988-1990	59	13	23	2	15	4	6	1	5	2	0.09	0.01
^b 1991-1993	105	18	21	5	21	2	7	1	9	1	0.10	0.01
^c 1994-1996	120	2	21	2	7	2	8	1	7	3	0.12	0.02
^d 1997-1999	140	6	17	2	4	1	9	3	15	3	0.15	0.01
^d 2000-2002	153	8	10	1	3	1	7	2	18	2	0.18	0.01

^{*} Mean yearly proportion of antlered deer observed by hunters on the opening 2-days of shotgun season (based on 342 ± 28 hunter hrs of observation/year).

^a Male fawns (MF) harvested per year.

^b No antler restrictions.

^c Prohibited harvest of males with <7 antler points.

^d Prohibited harvest of males with < 40-cm outside antler spread.

Table 2. Pre- (1994-1996) (Rosenberry et al. 1999) and post-QDM (2001-2002) estimates of emigration, survival, emigrants, immigrants, post-dispersal net difference, and collective behaviors of yearling male white-tailed deer during the breeding season at Chesapeake Farms, Maryland.

Parameter	<u>Pre-QDM</u>		<u>Post-QDM</u>		P-value
	Estimate	SE	Estimate	SE	
* YM Emigration	0.70	0.07	0.54	0.10	0.165
* YM Survival	0.44	0.07	0.72	0.08	0.005
^a Emigrants	39	8	28	5	0.395
^b Immigrants	31	11	37	7	0.741
^c YM Net difference	-8	14	+9	9	0.289
^d YM Agonistic AF	0.57	0.27	1.08	0.23	0.186
^e YM Breeding	2.58	0.41	1.34	0.45	0.053

* Proportion of yearling males (YM) 8 to 18 months of age.

^a Number of yearling males emigrating from study area during fall dispersal.

^b Number of yearling males immigrating onto study area during fall dispersal.

^c Net difference in number of yearling males post-fall-dispersal (immigrants – emigrants).

^d Mean yearling male (dispersers and nondispersers collectively) agonistic interactions (interactions/h) with adult females (AF).

^e Mean yearling male (dispersers and nondispersers collectively) breeding interactions (interactions/h).

Table 3. Yearling male disperser and nondisperser behaviors and antler points during pre-(1994-1996) (Rosenberry et al. 2001) and post-QDM (2001-2002) breeding seasons at Chesapeake Farms, Maryland.

Parameter	<u>Dispersers</u>		<u>Nondispersers</u>		<i>P</i> -value
	Mean	SE	Mean	SE	
^a YM Agonistic AF					
Pre-QDM	0.18	0.15	1.36	0.69	0.150
Post-QDM	0.99	0.27	1.12	0.32	0.812
^b YM Breeding YM					
Pre-QDM	3.21	0.40	0.99	0.55	0.005
Post-QDM	2.97	0.90	0.42	0.26	0.004
^c YM Antler points					
Pre-QDM	3.5	0.4	4.6	0.7	0.169
Post-QDM	4.3	0.5	2.5	0.2	0.002

^a Yearling male (YM) agonistic interactions (interactions/h) with adult females (AF).

^b Yearling male breeding interactions (interactions/h) with other yearling males.

^c Number of yearling male antler points.

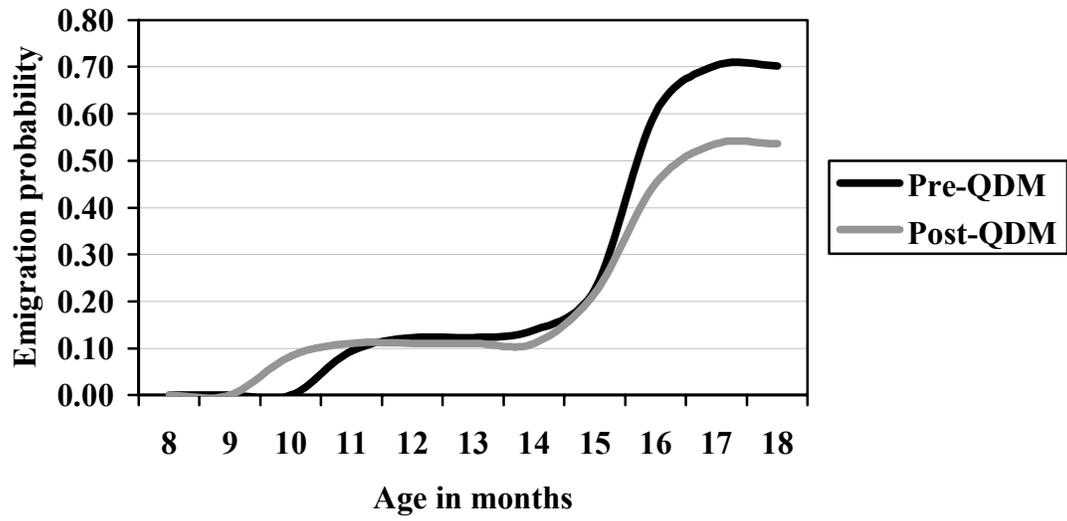


Figure 1. Emigration probability of yearling male white-tailed deer at Chesapeake Farms, MD, pre- (1994-1996) (Rosenberry et al. 1999) and post-QDM (2001-2002).

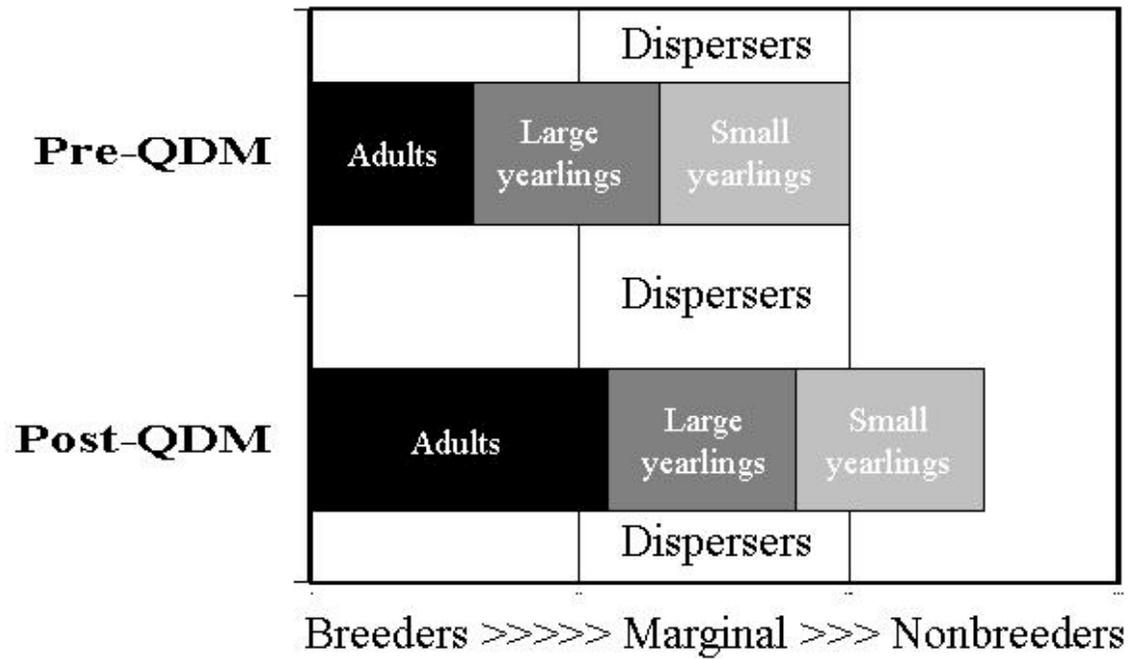


Figure 2. Conceptual model of the male breeding hierarchy in relation to dispersal of yearling male white-tailed deer at Chesapeake Farms, pre- (1994-1996) and post-QDM (2001-2002).

CHAPTER 2

Evaluation of the white-tailed deer genetic mating system at Chesapeake Farms, Maryland.

INTRODUCTION

Mating systems are characterized by numbers of successful matings, allocation of parental care, pair-bond duration, and tactics of selecting and acquiring mates; each ultimately varied to maximize lifetime reproductive success (Hughes 1998).

Reproductive success for polygynous males is strongly influenced by numbers of successful matings rather than the nurture of young (Trivers 1972). Pair bond duration, and individual tactics of acquiring and selecting mates varies with individuals, habitats, environments, and population demographics (Emlen and Oring 1977, Herrera and Macdonald 1993, Koprowski 1993) causing both inter- and intraspecific mating system variation (Zabel and Taggart 1989, Lott 1991).

Plasticity in white-tailed deer behaviors is common (Miller 1997); consequently, mating systems of white-tailed deer populations are likely variable. In a white-tailed deer population containing ample mature males, a strict dominance hierarchy is hypothesized to exist. Injury or death potentially reduces individual breeding lifespan, which inevitably reduces lifetime reproductive success (DeYoung et al. 2005). Male hierarchies are well-established prior to peak rut when the stakes of conflict are much higher, likely in part an evolutionary response to reduce frequency of intense fights that may cause injury or mortality (Brown 1974).

Age and antler size are related to position in the white-tailed deer male dominance hierarchy (Townsend and Bailey 1981), while breeding success is related to dominance

position in male cervids (Clutton-Brock et al. 1982, McElligot and Hayden 2000).

Intuitively, age and antler size are related to male breeding success in white-tailed deer. However, while dominance may guarantee privileges with estrous females, it does not necessarily equate to breeding success (Alexander and Borgia 1979). To ensure paternity of the female's offspring, dominant males must locate females at the onset of estrous, and effectively guard them from competing males throughout the estrous period.

The mating system of white-tailed deer typically entails formation of a tending bond between a breeding pair that encompasses the 24-hr estrous period of the breeding female (Hirth 1977). A small number of dominant, physically mature males (≥ 3.5 -years old) are hypothesized to monopolize tending bonds, effectively guarding estrous females from subordinate males, and controlling breeding opportunities (Hirth 1977, McCullough 1979, Marchinton and Hirth 1984). Subordinate males that attempt to form tending bonds are displaced by dominant males resulting in unsuccessful matings of subordinate males or multiple paternity in single litters (Sorin 2004). Hence, breeding success for subordinate males is restricted, and may be limited to surreptitious fertilization (DeYoung et al. 2002).

Mate selection may also play an important role in white-tailed deer mating systems, although the role of both female and male selection is unclear. Females may choose older males with large body and antler size, indicative of heritable quality genes (Ditchkoff et al. 2001, DeYoung et al. 2002). Additionally, multiple paternity may be the result of female selection, where females increase the probability that multiple offspring will receive quality genes by mating with multiple males when gene quality is highly variable (Petrie et al. 1998, DeYoung et al. 2002). Male breeding success is driven by

numbers of offspring; likewise male cervids may choose mature, highly productive females (Sorin 2004).

Information on white-tailed deer mating systems is based primarily on observations of courting behaviors made within enclosures, and inferred associative relationships of dominance status and breeding success (Hirth 1977, Marchinton and Hirth 1984, Miller et al. 1987, Ozoga and Verme 1985). Advances in molecular techniques and development of DNA microsatellite markers allow researchers to estimate parentage empirically with high confidence, and objectively investigate mating systems of free-ranging wildlife populations (Marshall et al. 1998, Anderson et al. 2002, DeYoung et al. 2003*a*). Breeding success across taxa inferred from behavioral observations is sometimes accurate (Gilbert et al. 1991, Pemberton et al. 1992, Dixon et al. 1993, Altmann et al. 1996). However, observed social mating systems often differ from actual genetic mating systems (Hughes 1998, Coltman et al. 1999, Worthington Wilmer et al. 2000, Gemmell et al. 2001) warranting tests of the current white-tailed deer mating system paradigm with molecular data. In addition, age specific breeding success is likely a function of population density, sex ratio, age structure, and habitat, warranting investigation of white-tailed deer mating systems of various population demographics and geographic areas.

Recent DNA paternity research fails to support the existing white-tailed deer mating system paradigm in which few dominant males monopolize breeding responsibilities. Multiple paternity of single litters in white-tailed deer is relatively common in enclosed populations (DeYoung et al. 2002, Sorin 2004), and likely exists in free-ranging populations, suggesting a single dominant male may sometimes fail to

secure tending bonds and effectively guard synchronous estrous females. In populations lacking mature males, breeding hierarchies may break down, resulting in equitable breeding success among young males (Ozoga and Verme 1985, DeYoung et al. 2004). In populations with ample mature males, DNA paternity research indicates males ≥ 3.5 -years old sire the majority of offspring. However, a large proportion of males breed, including young age-class males (DeYoung et al. 2004, Sorin 2004).

Our objectives were to investigate the genetic mating system of a free-ranging white-tailed deer population containing ample mature males by evaluating: (1) age-specific male breeding success; (2) relationships of body and antler size with breeding success of males ≥ 2.5 years old; (3) instances of multiple paternity in single litters; and (4) male and female mate selection. We hypothesized age, body size, and antler size strongly influenced breeding success if few dominant males monopolized breeding opportunities; multiple paternity did not occur if dominant males effectively located and guarded all estrous females; and dam and sire ages were correlated if age-specific mate selection occurred.

STUDY AREA

We conducted fieldwork from 1999-2003 at Chesapeake Farms (formerly Remington Farms), a 1,330-ha wildlife management and agricultural research and demonstration area operated by DuPont Crop Protection. Chesapeake Farms is located on the eastern shore of the Chesapeake Bay in Kent County, Maryland, 10 km southwest of Chestertown. The study area was approximately 50% forested with non-alluvial swamps that consisted predominately of oaks (*Quercus palustris*, *Q. alba*, *Q. phellos*, and *Q. rubra.*), sweetgum (*Liquidambar styracifula*), black gum (*Nyssa sylvatica*), and red

maple (*Acer rubrum*) with understory of greenbrier (*Smilax* spp.), sweet pepperbush (*Clethra alnifolia*), and highbush blueberry (*Vaccinium corymbosum*). Twenty percent of the study area consisted of crop fields with soybeans, corn, and winter wheat. Thirteen percent of the area consisted of fallow fields with a mix of orchard grass, clover, rye, and sunflowers. The remaining 17% of the area consisted of multiflora rose (*Rosa multiflora*) and other early successional species along with 80 ha of man-made waterfowl impoundments.

METHODS

Field techniques.--We captured deer ≥ 8 -months old January to early April 2001 and 2002 with a drop-net (Conner et al. 1987, Lopez et al. 1998). We blindfolded and sedated captured deer with an intramuscular dose of approximately 0.5 mg/kg of xylazine in 2001, and increased dosage to 2.0 mg/kg in 2002 to reduce capture induced mortality. Prior to release, each deer received an intramuscular dose of approximately 0.2 mg/kg of the xylazine antagonist yohimbine (Wallingford et al. 1996). Male fawns 8-10 months old received solar-powered ear tag radio transmitters with mortality sensors (ATS, Asanti, MN 55040). Neonates were also captured May-July 1994-2004. All deer received numbered monel ear tags.

We collected ear or tongue tissue from captured ($n = 122$) and harvested ($n = 621$) deer at Chesapeake Farms from September 2000 – July 2004. We isolated tissue samples with Qiagen® mini-spin columns following the recommended supplier protocol (DNeasy™ Tissue Kit; QIAGEN Genomics Inc.). We selected fifteen microsatellite markers (BM4208, BM6438, BM6506, BM848, Cervid 1, D, ETH152, ILSTS011,

INRA011, N, O, OarFCB193, OCAM, P, and Q) based on marker performances outlined in Anderson et al. (2002).

Single polymerase chain reactions (PCR) amplified fluorescent-tagged primers with a PE Gene Amp® 9600 thermocycler (Applied Biosystems Inc.). Mixtures for PCR amplification contained 5.00 µl Qiagen® HotStarTaq® Master Mix, 0.20 µl of 10 µM forward and reverse primers each, and 4.60 µl of 20 ng/µl DNA and H₂O, per reaction. Amplification conditions consisted of 15 min at 95 °C denaturation, 40 cycles of PCR, 50 sec at 95 °C denaturation, 50 sec at 60 °C annealing, 1 min 25 sec at 72 °C extension, 30 min at 72 °C extension, and held indefinitely at 4 °C. We diluted PCR products (1:60) with H₂O and pooled by a panel of 3 markers. We added size standard and formamide to pooled samples (*rox* 500; Applied Biosystems), and loaded pooled samples on an ABI Prism® 3700 DNA Analyzer (Applied Biosystems) for separation and detection. We analyzed DNA with GeneScan® (Applied Biosystems) and scored alleles with Genotyper® (Applied Biosystems).

We recorded dressed body mass, number of antler points, and antler spread for harvested males. Harvested deer ages were estimated from tooth wear and replacement (Severinghaus 1949), where lower mandibles were compared to known-aged deer mandibles at Chesapeake Farms. Known-aged deer consisted of deer captured and tagged as fawns (≤ 10 -months old) and later harvested at Chesapeake Farms from 1994 to 2003. Accurate age estimates from tooth wear and replacement are dependent on researcher experience, variations of wear patterns within age-classes, and variation of wear patterns across habitats. Despite recent scrutiny in age assignment of deer ≥ 3.5 -years old (Gee et al. 2002), we believe our age estimates are sufficiently accurate to

identify age classes for age-specific breeding success comparisons at Chesapeake Farms. Our site-specific experience and comparative methods with known-aged deer to account for intra age-class and habitat variation reduced bias in age estimates. Two or more researchers with more nearly 50 years combined experience of aging deer at Chesapeake Farms assorted lower mandibles into groups according to estimated age. Age classes included deer 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, 6.5, 7.5, and ≥ 8.5 -years old. Each lower mandible ≥ 2.5 -years old was compared with 28 known-age lower mandibles 2.5-8.5-years old.

Data Analysis--We tested loci Hardy-Weinberg equilibrium and pairwise loci linkage disequilibrium with GENEPOP 3.1 (Raymond and Rousset 1995) and adjusted $\alpha = 0.05$ using a sequential Bonferroni correction for multiple tests (Rice 1989). CERVUS 2.0 (Marshall et al. 1998) computed loci allelic richness, polymorphic information content, first parent exclusion probability, and observed and expected heterozygosity. We assigned paternity and maternity with CERVUS 2.0 (Marshall et al. 1998), and accepted most likely candidate parents at $\geq 80\%$ confidence, and ≤ 2 offspring/candidate parent loci mismatches.

All sampled deer born in a given year from 1999-2003 defined cohort offspring groups. For example, the 2001 cohort offspring group consisted of neonates captured in 2001, deer 8-10 months old captured in 2002, 0.5-year-old deer harvested in 2001, 1.5-year-old deer harvested in 2002, and 2.5-year-old deer harvested in 2003. White-tailed deer dispersal occurs predominately in yearling males whereas dispersal of males ≥ 2.5 years old is uncommon (Marchinton and Hirth 1984). Dispersal of yearling males at Chesapeake Farms occurred pre-breeding season, and breeding season occurred pre-

harvest season (Rosenberry et al. 1999). Breeding and harvest populations consisted of resident and immigrant males; therefore, we considered harvested males and resident radio-tagged yearling males as candidate sires, and excluded emigrant radio-tagged yearling males. Males in the population known to be alive and ≥ 1.5 -years old during the breeding season prior to the subsequent cohort offspring group parturition season defined candidate sire groups for each cohort offspring group.

We included some individual males as candidate sires in multiple years. For example, we included all 4.5-year-old males harvested in 2002 as 4.5-year-old candidate sires for 2003 offspring, 3.5-year-old candidate sires for 2002 offspring, 2.5-year-old candidate sires for 2001 offspring, and 1.5-year-old candidate sires for 2000 offspring. We likewise constructed candidate dam groups for each cohort offspring group by year and included some females as candidate dams in multiple years. Candidate dam groups consisted of females in the population known to be alive and ≥ 1.0 -year old during the cohort offspring group parturition season. We excluded captured deer >10 -months old in age-specific parentage analysis due to difficulties and unreliability in aging techniques of living deer.

Year specific parentage results from 1999-2003 did not differ and were pooled to increase statistical power for mating system evaluation. Because most individuals were considered candidate sires in multiple age-classes, we analyzed age specific breeding success and differences of least squares means with a mixed repeated measures model, SAS 8.2 (SAS Institute Inc., Cary, NC). Body and antler size data were not available for males prior to harvest; hence, body and antler size data occurred for individuals in a single year and did not include repeated measures. We did not include yearling males in

this analysis because we captured the majority of candidate yearling male sires at 8-10 months old or they were harvested at ≥ 2.5 -years old, therefore body and antler size data were not available at 1.5-years old. We had fewer data available for body and antler size, consequently we used a general linear model, SAS 8.2 (SAS Institute Inc., Cary, NC) to analyze body mass, antler points, and antler spread separately from age specific breeding success to provide greater statistical power for age specific breeding success analysis. Age-specific male breeding success comparisons consisted of males 1.5, 2.5, 3.5, and ≥ 4.5 -years old. Additionally, Pearson correlation coefficients for sire and dam ages were analyzed in SAS 8.2 (SAS Institute Inc., Cary, NC) to evaluate age-specific mate selection. Applicable results are presented as mean \pm SE.

RESULTS

Deer density prior to harvest was approximately 33 deer/km² (Shaw chapter 1). Harvest occurred primarily during a 2-week shotgun season (1999-2003) in late November and early December, with limited harvest during primitive weapons seasons during early fall and late winter. Selective male harvest based on antler criteria was initiated in 1994 (<7 points restricted harvest) and modified in 1997 (<40-cm outside spread restricted harvest). As a result of increased doe harvest and antler restrictions, the mean yearly proportion of antlered deer observed by hunters on the first 2 days of Maryland's shotgun season increased from 0.10 ± 0.01 (1989-93) to 0.19 ± 0.02 (1999-2003) ($t_8 = 4.01$, $P = 0.004$). The mean yearly harvest of males 1.5-years old decreased from 18 ± 3 (1989-93) to 3 ± 1 (1999-2003) ($t_8 = 4.94$, $P = 0.001$) while the mean yearly harvest of males ≥ 3.5 -years old increased from 7 ± 1 (1989-93) to 17 ± 2 (1999-2003) ($t_8 = 4.08$, $P = 0.004$). Reconstructed age-structures from harvest data (1999-2003)

indicated approximately 35% of the antlered population were ≥ 3.5 -years old. Over 600 hrs (2001-2002) of researcher observation supported estimated age-structures from harvest data, and indicated adult male to female ratios were approximately 1:1.5. Based on neonate captures ($n = 113$, 1999-2003) and behavioral observations, peak conception and birth occurred at approximately 12 November and 1 June respectively. Eighty percent of neonate captures from 1999-2003 occurred between 24 May and 8 June. Vaginal transmitter research indicated that parturition among 14 of 15 females occurred between 20 May and 3 June (J. L. Bowman, Department of Entomology and Applied Ecology at the University of Delaware, unpublished data), indicating most females came into estrous and were bred during an approximate 2-week rut.

Ten of 15 loci deviated significantly from Hardy-Weinberg equilibrium after a sequential Bonferroni correction for multiple tests (Table 1). Additionally, significant linkage disequilibrium existed for loci D and BM6438, D and ETH152, D and P, P and ILSTS011, P and BM6438, Q and OarFCB193, and ETH152 and OCAM after a sequential Bonferroni correction for multiple tests. Overall successful loci typing rate was 0.89, but was 0.64 for locus ILSTS011. Problematic markers (OarFCB193, OCAM, D, ILSTS011) were initially excluded in parentage analysis. Qualitative results of the conservative 11-marker analysis were similar to the complete 15-marker analysis; however, the 15-marker analysis provided greater statistical power for parentage assignment (total first parent exclusionary power, 0.9999) and was used.

CERVUS 2.0 assigned paternity to 209 of 431 offspring at $\geq 80\%$ confidence; however, offspring/candidate parent loci mismatches at $\geq 80\%$ confidence were 2.43 ± 0.11 . A more conservative parentage acceptance criteria at $\geq 80\%$ confidence, and ≤ 2

offspring/candidate parent loci mismatches produced qualitative results similar to parentage results at a strict acceptance criteria of $\geq 95\%$ confidence and ≤ 2 offspring/candidate parent loci mismatches. However the moderately conservative parentage assignment criteria at $\geq 80\%$ confidence, and ≤ 2 offspring/candidate parent loci mismatches yielded greater statistical power than the strict acceptance criteria of $\geq 95\%$ confidence and, ≤ 2 offspring/candidate parent loci mismatches, and was used for parentage analysis.

Paternity was assigned to 92 of 431 offspring under the moderately conservative acceptance criteria. The candidate sire sample consisted of 111 males 1.5-years old, 78 males 2.5-years old, 60 males 3.5-years old, and 44 males ≥ 4.5 -years old (Figure 1). Age was a significant factor for number of offspring sired in the repeated measures model ($F_{3, 148} = 4.33, P = 0.006$). The average 1.5-year-old male sired 0.20 ± 0.07 offspring, 2.5-year-old male sired 0.23 ± 0.08 offspring, 3.5-year-old male sired 0.45 ± 0.09 offspring, and male ≥ 4.5 -years old sired 0.56 ± 0.11 offspring (Table 2). Pairwise comparisons of least-squares means indicated 3.5 and ≥ 4.5 age-class males sired comparably more offspring than 1.5 and 2.5 age-class males (Table 3). There were no detectable differences in breeding success of 1.5 and 2.5-year-old males, and likewise no detectable differences in breeding success of 3.5 and ≥ 4.5 -year-old males.

A total of 92 offspring were sired by 17 males at 1.5-years old, 15 males at 2.5-years old, 16 males at 3.5-years old, and 14 males at ≥ 4.5 -years old. The number of annum offspring per successful sire was 1.16 ± 0.18 for males 1.5-years old, 1.18 ± 0.19 for males 2.5-years old, 1.77 ± 0.18 for males 3.5-years old, and 1.70 ± 0.20 for males ≥ 4.5 -years old. The maximum number of offspring detected by an individual in a single

breeding season was 4, by a single 3.5-year-old male. The sampled sire population consisted of 38% 1.5, 27% 2.5, 20% 3.5, and 15% ≥ 4.5 -year-old males. In comparison 22% of offspring were sired by males 1.5-years old, 21% by males 2.5-years old, 30% by males 3.5-years old, and 27% by males ≥ 4.5 -years old.

Seventy-seven sires ≥ 2.5 -years old were analyzed to evaluate the effects of body and antler size on breeding success. Body size (Type III F-test, $P = 0.206$), antler points (Type III F-test, $P = 0.602$), and antler spread (Type III F-test, $P = 0.561$) were not important factors in breeding success of males ≥ 2.5 years old in the general linear model ($F_{3,73} = 0.85$, $P = 0.471$, $R^2 = 0.031$).

We assigned both maternity and paternity to 41 offspring. Sire and dam ages were not correlated ($r = 0.006$). Yearling males bred females 4.1 ± 0.5 years old ($n = 10$), 2.5-year-old males bred females 3.1 ± 0.6 years old ($n = 9$), 3.5-year-old males bred females 3.9 ± 0.8 years old ($n = 10$), and males ≥ 4.5 years of age bred females 3.3 ± 0.5 years old ($n = 12$). Of 41 offspring with assigned maternity and paternity, we detected 4 pairs of twin offspring at ≥ 80 , ≤ 2 offspring/candidate parent loci mismatches. We observed multiple paternity in 2 of 4 sets of litters with sire ages of multiple paternity twins consisting of 3.5 and 7.5-years old, and 1.5 and 4.5-years old. Sire ages of single paternity twins were 3.5 and 4.5-years old.

DISCUSSION

CERVUS 2.0 assumes independent allele segregation and Hardy-Weinberg equilibrium. Several loci showed significant linkage disequilibrium, and a large proportion of Hardy-Weinberg equilibrium deviations occurred in the sampled loci. This may indicate population substructuring in which CERVUS 2.0 effectively carries out

parentage assignment, but confidence levels are distorted (Marshall et al. 1998).

Violation of CERVUS 2.0 likelihood estimator assumptions may result in confidence levels smaller than their suggested value. We used a relaxed confidence level ($\geq 80\%$) for paternity assignment to increase statistical power for mating system analysis. However, we censored the majority of CERVUS 2.0 parentage assignments at $\geq 80\%$ confidence due to high offspring/candidate parent loci mismatches, yielding moderately conservative parentage assignment and analysis that is likely better than the suggested 80% confidence level.

Our age-specific breeding success results are consistent with DNA paternity results in other white-tailed deer populations with $\geq 30\%$ of antlered deer ≥ 3.5 -years old (DeYoung et al. 2004, Sorin 2004). Older age-class males, particularly males ≥ 3.5 -years old had higher breeding success than younger age class males, supporting the hypothesis that breeding success is related to age, an important factor in dominance status (Townsend 1973). Seemingly, our results indicate a small proportion (21%) of males were successful sires. However, incomplete sampling of offspring and candidate sire populations occurred, and moderately conservative parentage assignment criteria were used. Therefore our estimates are sufficient for body size, antler size, and age-class comparisons, but should be viewed as minimum estimates of offspring sired and numbers of successful sires.

Approximately 60% of candidate sires in our population were sampled, and we expect approximately 60% of the sampled candidate sires were true sires of the sampled offspring. In comparison, only 21% of offspring were assigned paternity, indicating incomplete power to detect all paternities under our assignment criteria. In addition,

approximately 35% of offspring were sampled, indicating minimum estimates of breeding success. Given 21% successful paternity assignment, approximately 60% candidate sires sampled, and 35% offspring sampled, average annum offspring sired are likely closer to 1.6 ± 0.5 for 1.5, 1.8 ± 0.6 for 2.5, 3.7 ± 0.7 for 3.5, and 4.6 ± 0.9 for ≥ 4.5 -year-old males than conservative estimates presented in our results {likely offspring sired estimate = conservative offspring sired estimate * 0.6 / (0.35 * 0.21)}.

Likewise the proportion of successful males is likely much greater than 21%, demonstrating numerous males share breeding responsibilities. At Chesapeake Farms, at least 14 males in each age-class successfully bred, and the maximum observed offspring sired by an individual in a single breeding season was 4. Additionally, success was not related to weight or antler size of males ≥ 2.5 -years old, factors indicative of dominance status (Geist 1966, Townsend 1973).

Conceivably, because age was related to body and antler size at Chesapeake Farms (Rosenberry 1997), and age was an important predictor in breeding success, a relationship should exist between body size, antler size, and breeding success. Additionally, male white-tailed deer have evolved elaborate secondary sexual characteristics, which conceptually support the notion of increased breeding opportunities for individuals with larger bodies and antlers. However, our data did not support this intuitive relationship, indicating body and antler size were not strongly related to breeding success. In part, failure to detect this relationship may be attributed to our relatively small sample size ($n=77$) and lack of repeated measures in our body and antler size analysis. Nonetheless, if few dominant males monopolize breeding opportunities, a

strong detectable relationship conceivably would exist between body size, antler size, and breeding success.

Multiple paternity of single litters also occurred, comparable to results in penned (DeYoung et al. 2002) and enclosed populations (Sorin 2004). Instances of multiple paternity additionally indicates that few dominant males cannot effectively locate, guard, and breed all estrous females, at least under the observed adult sex ratio at Chesapeake Farms. These results fail to support the prevailing paradigm where few dominant males monopolize breeding opportunities (Hirth 1977, Marchinton and Hirth 1984).

Efficacy of dominant male breeding monopolization is likely related to age-structure, sex ratios, and estrous synchrony (Sorin 2004). At Chesapeake Farms (1999-2003) there were ample mature males, and adult male to female ratios were relatively balanced. Estrous synchrony was high, where most females were bred during an approximate 2-week rut. Instances of multiple paternity, and breeding success of numerous males across age-classes, weight, and antler sizes suggest there are limits to the number of females a dominant male can monopolize. A single dominant male may try to monopolize female groups with as many as 10 females (Marchinton and Hirth 1984). However, breeding pairs isolate themselves (Hirth 1977), reducing an individual male's capacity to concurrently guard more than one estrus female. A female will stand for copulation for approximately 24 hrs (Marchinton and Hirth 1984). Given relatively extensive pre- and post-copulatory stages that involve seeking, chasing, and guarding estrus females (Hirth 1977), and individual male may court a single female for upwards of 48 hrs. Therefore, a single dominant male cannot feasibly monopolize more than roughly 7-10 females in a single breeding season when estrous synchrony is high and rut

duration is short. Subordinate males benefit from this limit, and breed surplus females that dominant males fail to locate and tend.

Subordinate male breeding success may increase in heavily female skewed populations because the number of surplus females likely increases. Heavily female skewed populations with young male dominated age-structures may further increase subordinate male breeding success. Dominance hierarchies likely exist in most white-tailed deer populations, though the degree of dominance hierarchies may vary from strict to relaxed depending on population age-structure. In addition, dominance hierarchies do not necessarily conform to breeding hierarchies. In populations with an older male age-structure, a strict dominance hierarchy exists where age and size influence dominance rank (Townsend 1973, Marchinton and Hirth 1984). Our data suggest breeding hierarchies are conversely more relaxed, where age appears to be the most important factor in breeding success, at least until males reach 3.5 years of age. In populations with a younger male age-structure, antler size influences dominance rank of young males (Rosenberry 1997); however, most males are the same age, hence dominance hierarchies are likely more relaxed, and consequently breeding hierarchies are further relaxed. In female skewed populations that lack mature males, young males adequately sire most females, however young males lack strict dominance hierarchies and ritualized courtship and scent marking behaviors (Ozoga and Verme 1985). As a result equitable breeding success for young males occurs (DeYoung et al. 2004).

At the onset of increased doe harvest and antler restrictions at Chesapeake Farms (1994-1996), a female skewed and young male age-structured population existed (Shaw chapter 1). Eighty percent of neonate captures ($n = 77$) occurred between 26 May and 11

June indicating high estrous synchrony and short rut duration occurred. A dominance hierarchy also occurred where adult males, large antlered yearlings, and small antlered yearlings respectively tended to be dominant in sparring and present threat interactions (Rosenberry 1997). However, because the dominance hierarchy was likely relaxed, and young males lacked ritualized courting and scent marking behaviors, dominant young males in the young male age-structured population (1994-1996) were likely less effective in locating and guarding estrous females than dominant mature males in the older age-structured population (1999-2003). As a result, young age-structured populations may have an elevated surplus of estrous females available for subordinate male breeding. Potential break down of dominance hierarchies and increases in the proportion of young males likely increases the average subordinate male breeding success in populations where high estrous synchrony occurs. However, in southern populations where prolonged breeding seasons and low estrous synchrony is typical (Marchinton and Hirth 1984), dominant males may be more effective in guarding estrous females, hence there are fewer surplus females, and subordinate male breeding success is lower.

We present results on per capita age-specific breeding success and age-specific contributions to our offspring sample. We believe inferences from these results can be made to age-specific contributions to the offspring population. Selective harvest could potentially bias our candidate sire sample because males that did not meet minimum antler restriction criteria were not vulnerable to harvest and could be misrepresented in our sample. However, sampling occurred over a 5-year period, where harvest of older age-class males yielded sampling of the same individuals at younger age-classes. Additionally, drop-net captures in 2001 and 2002 supplemented sampling of young age-

class males. The composite sampled candidate sire population was constructed via population reconstruction from captured and harvested males 1999-2003. The age-structure of sampled candidate sires was similar to the age-structure of males estimated from over 600 hours of field observations in 2001 and 2002 (J. C. Shaw, unpublished data), which supports the notion that the sampled candidate sire population age-structure was representative of the actual candidate sire age-structure.

While individual breeding success was significantly related to age, collective age-specific contributions to the population were similar. In our sample 1.5-year-olds collectively contributed 20 offspring, 2.5-year-olds 19, 3.5-year-olds 28, and 4.5-year-olds 25 offspring to the sampled offspring population. This suggests the average young male makes a significantly smaller contribution to the population than a mature male, however young males collectively make genetic contributions comparable to older age classes to the population because there are more of them.

In contrast to Sorin's (2004) results where yearling males tended to breed with yearling females, yearling males at Chesapeake Farms bred with females of various ages, and no correlation existed between male and female breeding pair ages. The demographic population of the George Reserve deer herd, Michigan, (Sorin 2004) was similar to the Chesapeake Farms population (1999-2003). At the George Reserve, yearling male breeding success with yearling females was hypothesized to be attributed to close associations of yearling males with yearling females (Marchinton and Hirth 1984), and disproportionate breeding efforts of mature males towards older and more productive females (McCullough 1979, Sorin 2004). Based on vaginal transmitter research, virtually all females ≥ 1.5 -years old at Chesapeake Farms bred (J. L. Bowman,

Department of Entomology and Applied Ecology at the University of Delaware, unpublished data). Dominant males plausibly will selectively breed older more productive females to maximize offspring when breeding competition is high, and numbers of successful matings are limited (Clutton-Brock 1988, Sorin 2004), while subordinate males sire less productive surplus females. However, our results indicated either older males did not selectively breed older females at Chesapeake Farms, or they failed to successfully monopolize tending bonds with older females.

The function of female selection is additionally ambiguous (DeYoung et al. 2002). Multiple paternity may be linked to female selection rather than surreptitious fertilization or subordinate male displacement. In populations with high male genetic variability, mating with a single male reduces genetic diversity of twin offspring, where quality offspring genetics are dependent on the genes of a single male. Mating with several males increases genetic diversity of offspring and increases the probability of quality phenotypes in multiple offspring, giving an advantage to females that choose to mate with multiple males (Petrie et al. 1998, DeYoung et al. 2002). If female choice is the cause of multiple paternity, females conceivably would breed with multiple dominant males. However, relatively large discrepancies in ages (≥ 3 years) were observed in sires of multiple paternity twins at Chesapeake Farms, and have been observed in other populations (DeYoung et al. 2002, Sorin 2004), supporting male competition as the cause of multiple paternity rather than female selection. Additionally, behavioral observations (Hirth 1977) support the displacement hypothesis (Sorin 2004) where multiple paternity occurs when a younger subordinate male secures a tending bond and breeds with a

female, and is subsequently displaced by an older dominant male who resumes the tending bond and breeds with the female.

Female cervids may selectively breed large-antlered males in some populations (Bubenik 1983), and avoid breeding with young males (Clutton-Brock et al. 1982). However, female selection based on male antler or body size is not universally apparent (Clutton-Brock et al. 1982). Neither body nor antler size at Chesapeake Farms were important predictors of breeding success of males ≥ 2.5 -years old, indicating deficient female selectivity based on these factors. However, male age was an important factor in breeding success. Our age-specific male breeding success results are either attributed to dominance status and increased breeding authority of older males, increased female selectivity towards older males, or a combination of the two.

Age is related to dominance rank among females (Townsend 1973). In populations with high estrous synchrony of females, we would expect older dominant females to mate with older dominant males, if female selection occurred. No correlation between breeding pair ages existed in the synchronous estrous population at Chesapeake Farms, therefore female selection inadequately explained the age-specific relationship of male breeding success. Our results did not support age-specific male and female mate selection, and indiscriminate breeding occurred post-procurement of male dominance status.

Our results indicate a breeding hierarchy does exist in the mature age-structured Chesapeake Farms population, where older age class males have higher breeding success than younger age class males. However, this breeding hierarchy is not as strict as perceived by previous observation research (Hirth 1977). Young age-class males have

lower average breeding success than older males, nevertheless young males do breed, and collectively contribute offspring comparable to older age class males. In addition, numerous males ≥ 3.5 years of age breed, regardless of weight or antler size.

Observation research indicates a strict dominance hierarchy exists in populations with ample mature males. However, dominance does not necessarily equate to breeding success. While acquiring dominance rank and subsequently guarding mates may be the most effective way of maximizing breeding success in male white-tailed deer, surreptitious fertilization of surplus females, which dominant males fail to effectively locate and tend, may serve as a viable alternative strategy for subordinate males until dominance status is acquired, particularly when estrous synchrony is high. In addition, we found no evidence of male or female selection, indicating matings are largely indiscriminate opportunistic events, where breeding success is driven by numbers of successful matings and the ability of young males to locate surplus females, and the ability of dominant males to locate and guard estrous females.

MANAGEMENT IMPLICATIONS

Our results show that individual males ≥ 3.5 -years old have higher breeding success than individual males ≤ 2.5 -years old. However, numerous males across age classes bred, and young age-class males collectively contributed offspring comparable to older age-class males. Body or antler size were not significant factors in breeding success of males ≥ 2.5 -years old, multiple paternity occurred, and mate selection was not evident. Given the preponderance of female philopatry (Marchinton and Hirth 1984), if white-tailed deer mating systems were characterized by dominant male monopolization of related harems, then we would expect relatively low genetic variability within

populations. Conversely, white-tailed deer have the highest genetic variation of large grazing mammals (Smith et al. 1984, Breashears et al. 1988) and high levels of heterozygosity exist within populations (DeYoung et al. 2003*b*). High genetic diversity within populations can be attributed to gene flow, but may be in part attributed to relaxed breeding hierarchies and significant genetic contributions by many.

Consequently, harvest management strategies aimed to “improve” genetics through culling of “genetically inferior” males may not be effective, particularly in free-ranging populations. Antler characteristics are dependent on a variety of environmental and genetic factors, where degrees of heritability of antler traits are variable among populations and age-classes (Williams et al. 1994, Lukefahr and Jacobson 1998). Heritability of antler traits is low for yearling males in comparison to mature males (Lukefahr and Jacobson 1998), consequently harvest strategies aimed to cull “genetically inferior” yearlings may not be effective in populations where environmental sources of variation dictate antler development. Management regimes that aim to improve herd genetics by culling “genetically inferior” males at mature ages may also be impacted by collective genetic contributions of cull males preceding harvest. The degree of “genetically inferior” male harvest needed to manipulate population genetics is unclear, where extensive harvest of young males may contradict allied management objectives to improve sex ratios and male age-structures.

Additionally, in populations with high estrous synchrony, dominant males fail to monopolize tending bonds and young males breed surplus females, collectively making genetic contributions comparable to older males. At Chesapeake Farms, a relatively balanced adult sex ratio and mature male age-structure existed. A mature age-structure

and intense breeding competition did not ensure immense genetic contributions from dominant, “genetically superior” males. The number of adult males may have to exceed the number of adult females in order for older dominant males to collectively contribute more genes than younger subordinate males. In populations where the number of males exceeds the number of females, the number of surplus females available for subordinate males is likely lower, assuring a higher proportion of dominant male genes into the population.

Pre-colonial white-tailed deer populations likely had mature age-structures and relatively balanced adult sex ratios, comparable to the Chesapeake Farms population. Under pre-colonial population demographics, genetic contributions by many and high genetic diversity likely existed. Genetic diversity and the ability to adapt to dynamic environmental and human induced pressures contribute to the resilience of white-tailed deer populations across North America (Smith et al. 1984). Management practices that aim to streamline genetics and produce trophy bucks through culling may compromise genetic diversity, which characterizes the species.

Likewise, strict “shoot-don’t shoot” harvest practices based on antler restriction criteria may inadvertently manipulate population genetics by applying differential male harvest pressures (Strickland et al. 2001). Dominant “genetically superior” males meet antler restriction criteria at relatively young ages and are more vulnerable to harvest. Subordinate “genetically inferior” males may take many years, and in some situations may never reach minimum antler size harvest criteria. Hence, lifetime reproductive success is higher for subordinate “genetically inferior” males. Consequently, these males may collectively account for the majority of genes expressed in subsequent populations,

and adversely impact the frequency of quality genes. Conversely, dominant “genetically superior” males in pre-colonial populations were not selectively harvested at young ages. Hence, they had high life-time reproductive success and made significant genetic contributions to pre-colonial populations. To ensure future genetic diversity comparable to pre-colonial populations, harvest pressures that mimic natural mortality, and discriminate on age rather than antler size may be warranted.

Restoration management strategies including translocations or reduction of dispersal barriers may be effective practices for improving population genetics by increasing genetic diversity in isolated populations. Small genetic contributions from a few individuals can effectively increase genetic diversity (Smith et al. 1984). Assuming translocated or emigrant males survive to breeding age, the probability of breeding success of an established male is relatively high, and increases with age, hence genetic restoration management is promising.

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Table 1. White-tailed deer population genetics at Chesapeake Farms, Maryland from 746 individuals genotyped with microsatellite DNA markers (1999-2003).

Locus ^a	Alleles ^b	Size range ^c	Samples ^d	H _o ^e	H _e ^f	P-value ^g	PIC ^h	P _E ⁱ
BM4208	16	140-183	648	0.74	0.80	<0.001	0.78	0.46
BM6438	14	250-281	708	0.88	0.85	0.200	0.84	0.55
BM6506	12	173-210	688	0.61	0.87	<0.001	0.85	0.58
BM848	11	363-393	705	0.56	0.85	<0.001	0.83	0.52
Cervid1	13	160-196	583	0.87	0.87	0.490	0.85	0.58
ETH152	11	169-205	685	0.42	0.83	<0.001	0.81	0.50
ILSTS011	6	260-271	475	0.36	0.51	<0.001	0.42	0.13
INRA011	5	192-202	676	0.52	0.51	0.110	0.45	0.13
OarFCB193	13	93-125	726	0.75	0.78	<0.001	0.76	0.43
OCAM	16	177-225	606	0.79	0.82	0.033	0.80	0.50
D	8	155-192	708	0.57	0.76	<0.001	0.74	0.39
N	16	292-343	697	0.73	0.88	<0.001	0.87	0.62
O	5	181-202	675	0.70	0.64	<0.001	0.57	0.22
P	9	211-240	676	0.49	0.80	<0.001	0.77	0.44
Q	17	227-287	731	0.88	0.88	0.697	0.87	0.62

^a Locus name

^b Number of alleles per locus

^c Size range of alleles in nucleotides (with primer)

^d Samples successfully genotyped

^e Expected heterozygosity

^f Observed heterozygosity

^g Hardy-Weinberg equilibrium test P-value

^h Polymorphic information content

ⁱ First parent exclusion probability

Table 2. Minimum age-specific breeding success of male white-tailed deer at Chesapeake Farms, Maryland (1999-2003).

	1.5 ^a		2.5 ^a		3.5 ^a		≥4.5 ^a		Total	
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
Offspring sired	0.20	0.07	0.23	0.08	0.45	0.09	0.56	0.11	0.30	0.05
Successful sires	0.16	0.04	0.18	0.05	0.26	0.05	0.33	0.06	0.21	0.03
Offspring/successful sire	1.16	0.18	1.18	0.19	1.77	0.18	1.70	0.20	1.43	0.11

^a Age class by years of age

Table 3. Age-specific breeding success comparisons of male white-tailed deer at Chesapeake Farms, Maryland (1999-2003).

Age A ^a	Age B ^a	LSD ^b	SE	P-value
1.5	2.5	-0.029	0.093	0.759
1.5	3.5	-0.255	0.102	0.013
1.5	≥4.5	-0.364	0.123	0.004
2.5	3.5	-0.227	0.107	0.035
2.5	≥4.5	-0.335	0.126	0.009
3.5	≥4.5	-0.108	0.130	0.406

^a Age class by years of age

^b Least squares difference of Age class A and Age class B mean offspring sired

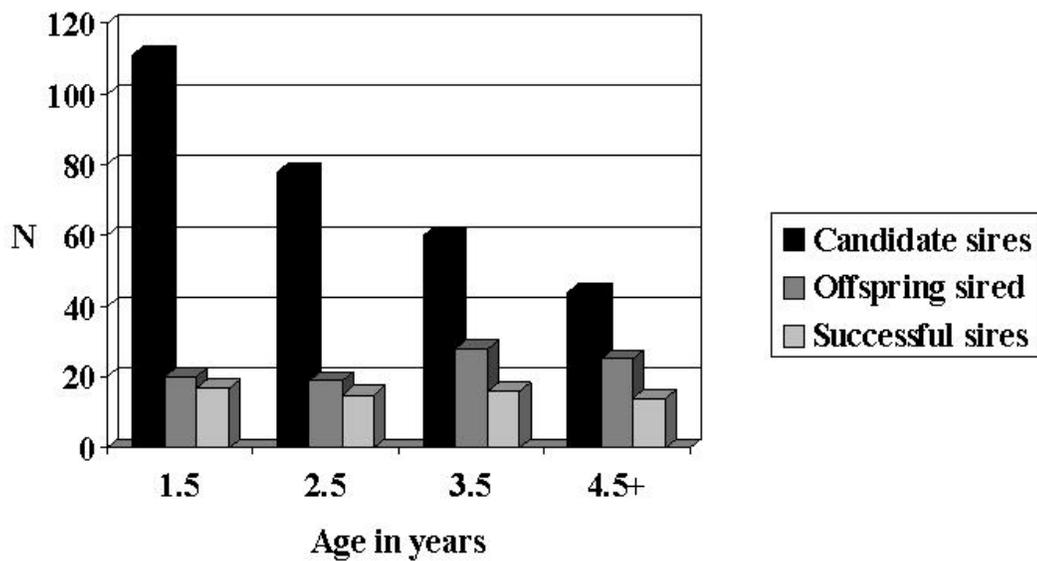


Figure 1. Male white-tailed deer breeding success at Chesapeake Farms, Maryland determined by genetic paternity analysis. Candidate sires consist of DNA sampled males from 1999-2003. Age-specific number of offspring sired and successful sires are minimum estimates due to incomplete sampling of offspring and sire populations, and conservative parentage assignment criteria.

CONCLUSION TO THE DISSERTATION

Reliable management decisions are dependent on evaluations of population processes. The implications of QDM on population processes are complex, and likely vary across landscapes and populations. At Chesapeake Farms, changes in population demographics through QDM impacted deer social pressures by decreasing yearling male breeding behaviors. Consequently, dispersal ecology was affected. An increased number of adult males may have decreased dispersal, and increased site-specific management efficiency in protecting young males from harvest. However, nondisperser yearling males had fewer antler points than dispersers, which may compromise management objectives to increase male antler quality.

The long-term effects of this observed phenomenon on antler phenotypes needs further assessment. Specifically, Chesapeake Farms should continue detailed harvest data collection and monitor age-specific deer weights and antler dimensions to assess long-term trends in age-specific antler quality. In addition to body size, antler spread, and antler point data, estimates of Boone and Crockett antler scores may provide an additional data source for future comparisons of antler quality. If differential dispersal rates of poor and high quality yearlings impact population antler quality, then changes in age-specific antler quality are expected over time, engaging a testable hypothesis; (1) the current preponderance of quality yearling male dispersal negatively impacts age-specific antler quality of males harvested at Chesapeake Farms.

Wildlife science is imperfect, where confounding factors can confuse interpretation of results. Among those factors, continued improvement in habitat and harvest management practices at Chesapeake Farms may obstruct detectability of changes

in quantitative antler traits caused by differential dispersal rates of quality yearlings. Conversely, an observed decreasing trend in antler quality of males harvested may be attributed to selective harvest criteria rather than a preponderance of quality yearling male dispersal. In addition to posing sampling issues, selective harvest may also have direct impacts on the mating system at Chesapeake Farms, and consequently affect population genetics and antler quality, further confounding result interpretation. Comparison of life-time genetic contributions of poor and high quality males may provide further insight into long-term trends in observed age-specific antler quality.

The mating system in the QDM herd at Chesapeake Farms differed from the prevailing observation based mating system paradigm where few dominant males ≥ 3.5 -years old monopolize breeding responsibilities. Numerous males across age-classes bred, and antler or body size were not predictors of breeding success of males ≥ 2.5 -years old. Lifetime reproductive success is a function of collective progeny produced over the course of an individual's life. Intuitively, individuals that live longer have higher lifetime reproductive success than individuals who are short lived. Our results indicate lifetime reproductive success for white-tailed deer may be strongly influenced by age rather than dominance.

Ideally, harvest pressure should discriminate on age rather than antler dimensions. Conversely, Chesapeake Farms like many QDM programs promotes a strict "shoot-don't shoot" policy based on antler dimensions to appease inexperienced hunters. As a result, high antler quality males meet antler restriction criteria and are vulnerable to harvest at earlier ages than poor antler quality males. Poor antler quality males consequently may have higher lifetime reproductive success than high antler quality males.

The long-term implication of antler biased selective harvest on antler quality also warrants further evaluation. Specifically, average Boone and Crockett antler scores for each age-class should be evaluated, where less than average males are considered poor quality males, and above average males are considered high quality males. Continued DNA sampling of Chesapeake Farms populations will eventually lead to near complete sampling of preceding populations, and allow a thorough assessment and comparison of the lifetime genetic contributions of poor and high quality males, engaging a second testable hypothesis; (2) current selective harvest criteria favors significantly more lifetime genetic contributions from poor quality males.

Lastly, future research opportunities exist to investigate multiple paternity at Chesapeake Farms. We observed multiple paternity of single litters at Chesapeake Farms; however, our small sample size ($n=4$) did not allow a precise estimate of the frequency of multiple paternity. DNA fetal sampling of late-season harvested females could increase competence in parentage assignment, and allow a more complete evaluation of the frequency of multiple paternity in a free-ranging population, engaging a third hypothesis; (3) multiple paternity in free-ranging populations is common.

Our research has advanced understanding of the implications of QDM on white-tailed deer population demographics, social pressures, dispersal ecology, and mating systems. However, as commonly observed in research endeavors, the more we learn, the more we need to know. The increased tendency for large antlered yearlings to disperse, and the significant genetic contributions of subordinate males may have long-term effects on antler quality on QDM properties, warranting continued monitoring of population genetics and antler development at Chesapeake Farms.

APPENDIX 1

Modified version of the portable drop net described by Lopez et al. (1998)

A braided nylon rope was loosely threaded around the perimeter of a 30 ft X 30 ft nylon net. Washers were tied at both ends of the braided rope at the designated trigger corner. Another braided nylon rope was threaded through the center of the 30 ft X 30 ft net from the trigger corner to the opposite corner. A washer was tied to the trigger corner end, and a loop was tied in the opposite end of the rope. A 1 ft ground rod was driven in the ground near all 4 corners of the net with approximately 4 inches remaining above ground. The ground rods were driven approximately 3 ft from the corners of the fully extended net and near a tree with >3 inch diameter if feasible. Finding 4 trees that created a perfect square at the appropriate distances was difficult; so 3 trees that created a right angle were typically used. A 6 ft galvanized pole was placed on top of each ground rod. A hole was drilled at the top of the galvanized pole at the designated trigger corner. The braided nylon perimeter rope was threaded around each pole leaving the actual net unconnected to the poles. The looped end of the center rope was placed around the pole opposite the trigger corner. The galvanized pole without an adjacent tree was grounded at an approximate 60 degree angle away from the net. The other 3 poles were stabilized by placing ratchet straps above the nylon braded rope and around the adjacent tree and pole. Both ends of the perimeter rope as well as the unlooped end of the center rope were pulled tight and fastened to the trigger pole by placing a trigger pin through all three washers and into the drilled hole on the trigger corner pole. The net was completely suspended by tension created between the perimeter rope, center rope, and corner poles. To increase net tension, the corners were ratcheted and a 6 ft center post was used. The

net was tripped by pulling the trigger pin with a trigger wire from a tree stand approximately 30 yards away.

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Lopez, R. R., N.J. Silvy, J. D. Sebesta, S. D. Higgs, and M. W. Salazar. 1998. A Portable drop-net for capturing urban deer. Proceedings of the Annual Conference of Southeastern Association of Fisheries and Wildlife Agencies 52:206-209.

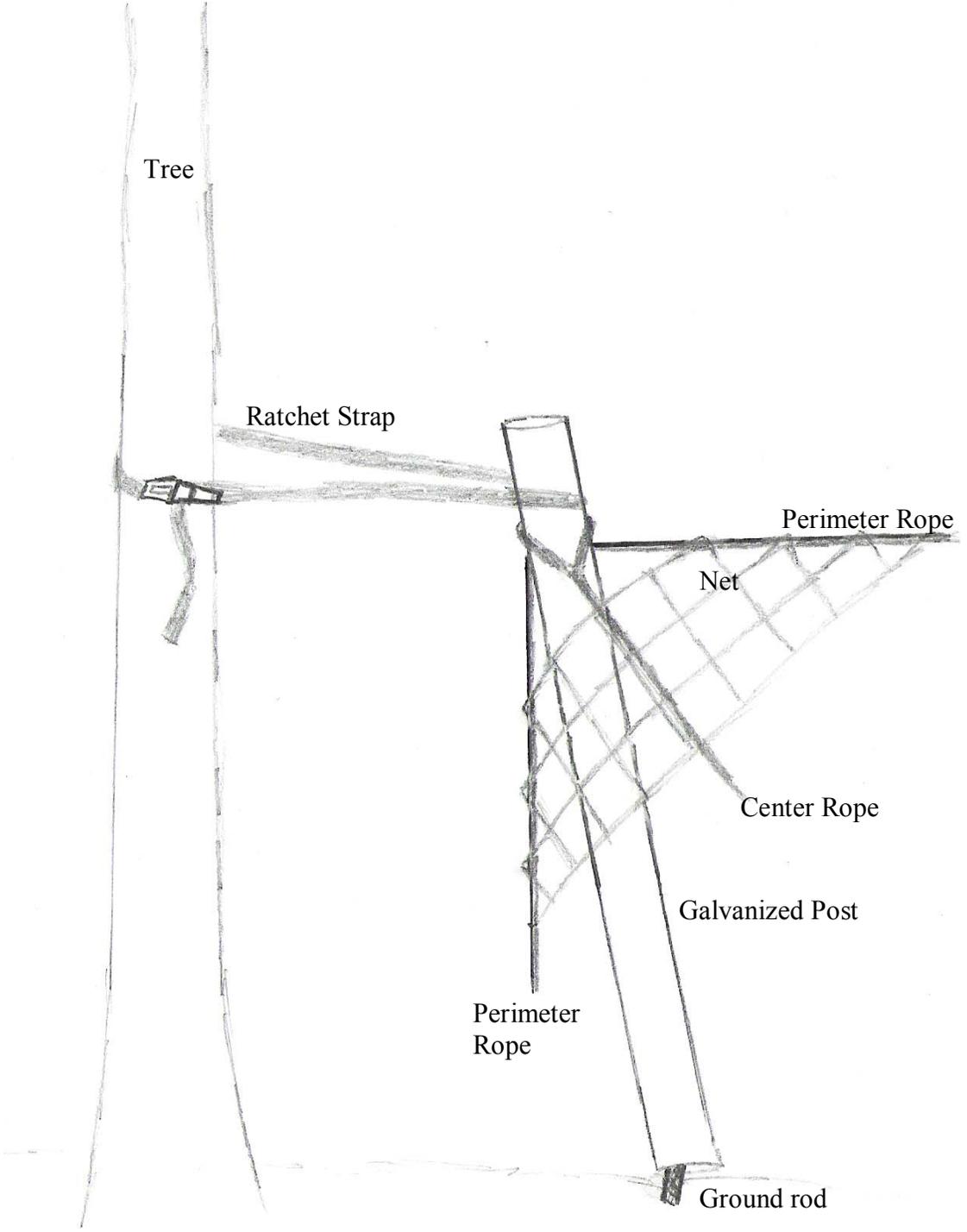


Figure 1: Corner opposite trigger

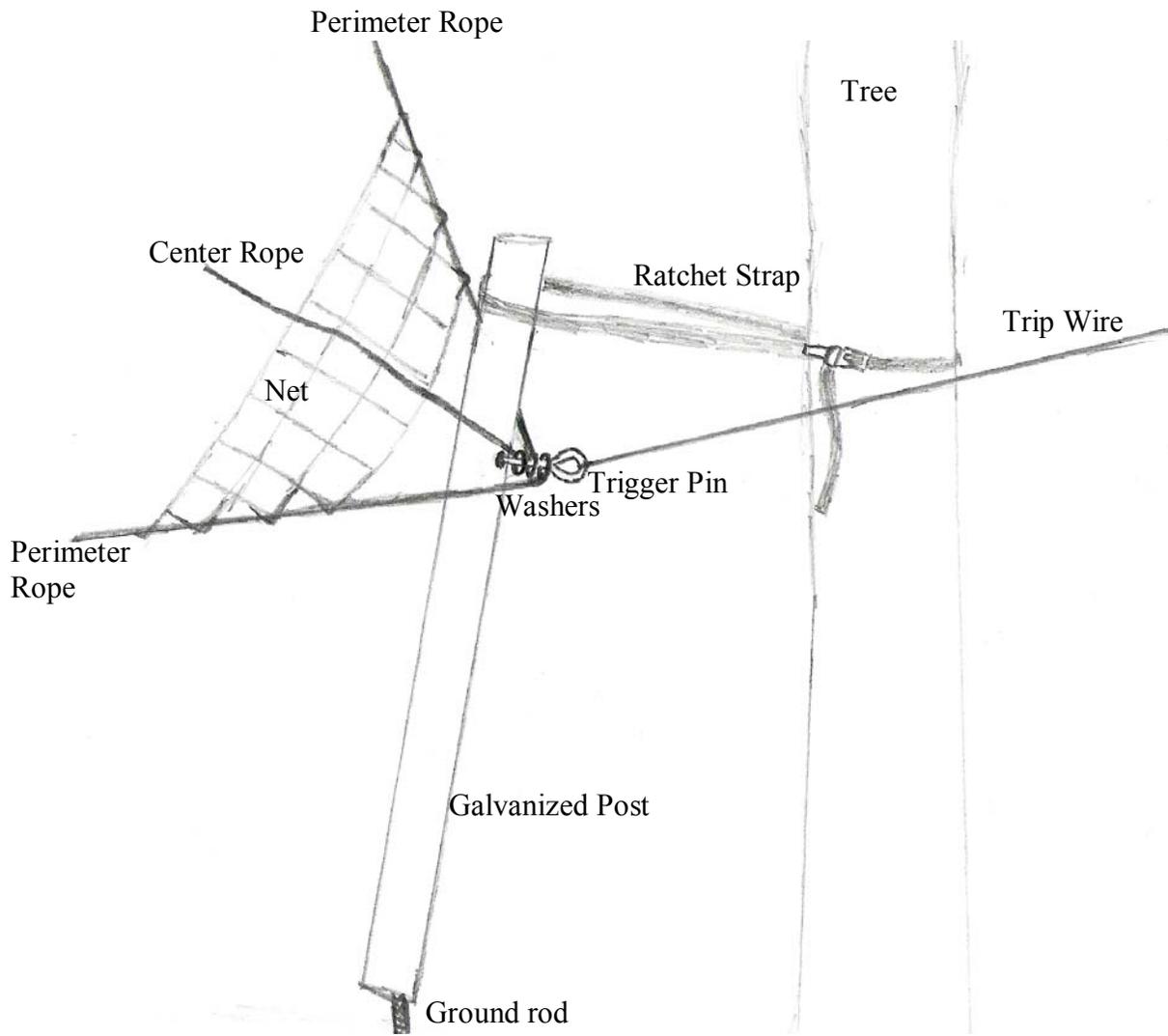


Figure 2: Trigger corner

APPENDIX 2

Table 1. 2001 and 2002 drop-netting success of adult bucks (AB), adult does (AD), male fawns (MF), and female fawns (FF) captured per effort hour. Mortalities noted are net related and do not exclude probable capture myopathy.

2001									
Method	Total Deer	AB	AD	MF	FF	Hours	Deer/Hour	Mortality	Mortality Rate
80ft.net/Field	57	3	19	19	16	127.7	0.45	7	0.12
Total	57	3	19	19	16	127.7	0.45	7	0.12
2002									
Method	Total Deer	AB	AD	MF	FF	Hours	Deer/Hour	Mortality	Mortality Rate
30ft.net/Woods	18	0	1	13	4	64.5	0.28	2	0.11
80ft.net/Field	27	2	7	12	6	40.3	0.67	3	0.11
Total	45	2	12	25	10	104.8	0.43	5	0.11

Table 2. Observation time periods.

Time period	Start date	End date
Pre-breeding1 (PB1)	June 18	July 15
Pre-breeding2 (PB2)	July 16	August 12
Breeding1 (B1)	August 13	September 9
Breeding2 (B2)	September 10	October 7
Breeding3 (B3)	October 8	November 4

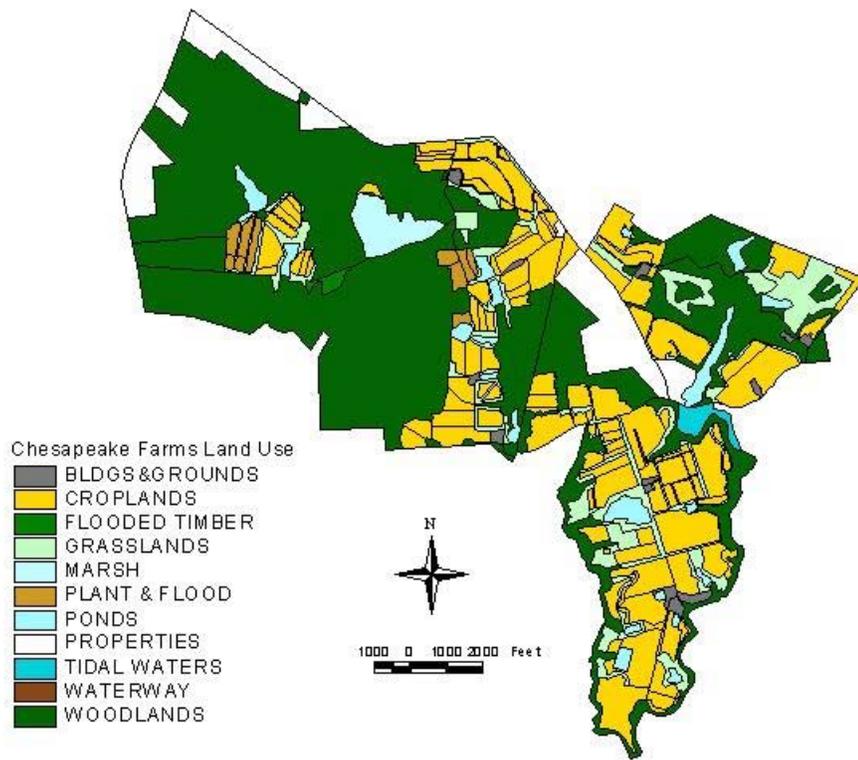


Figure 1: Chesapeake Farms, MD property boundary and land use.

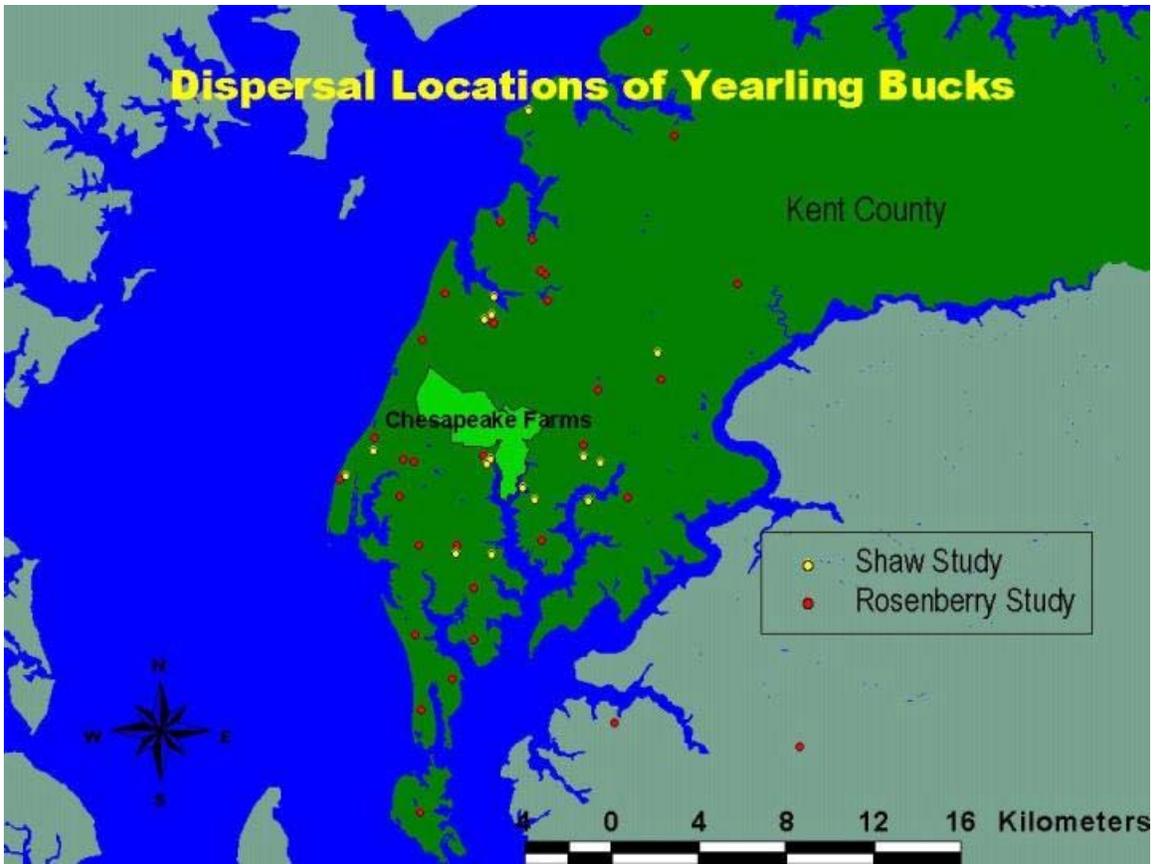


Figure 2: Location of emigrant yearling males post-dispersal

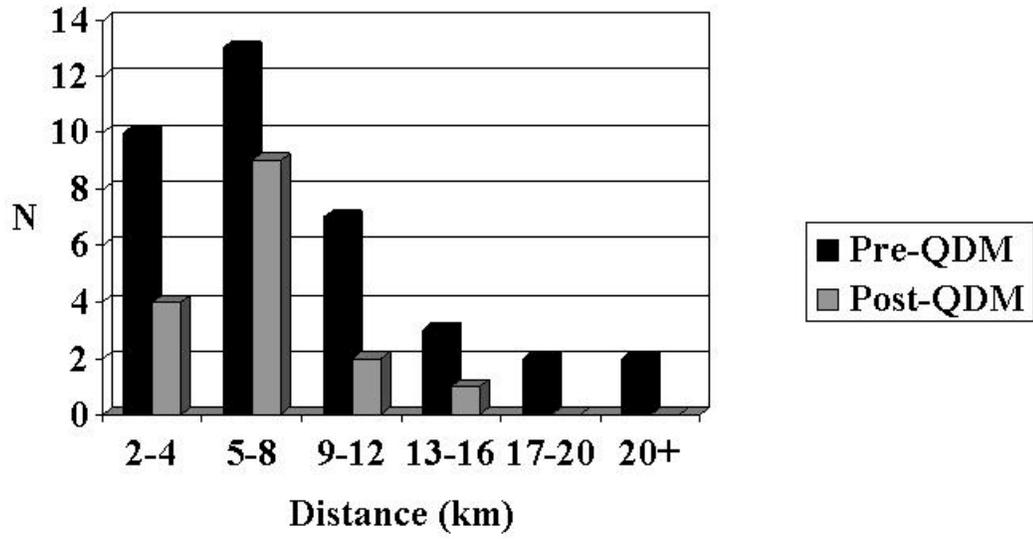


Figure 3: Pre-QDM (Rosenberry 1997) and post-QDM yearling male dispersal distances.

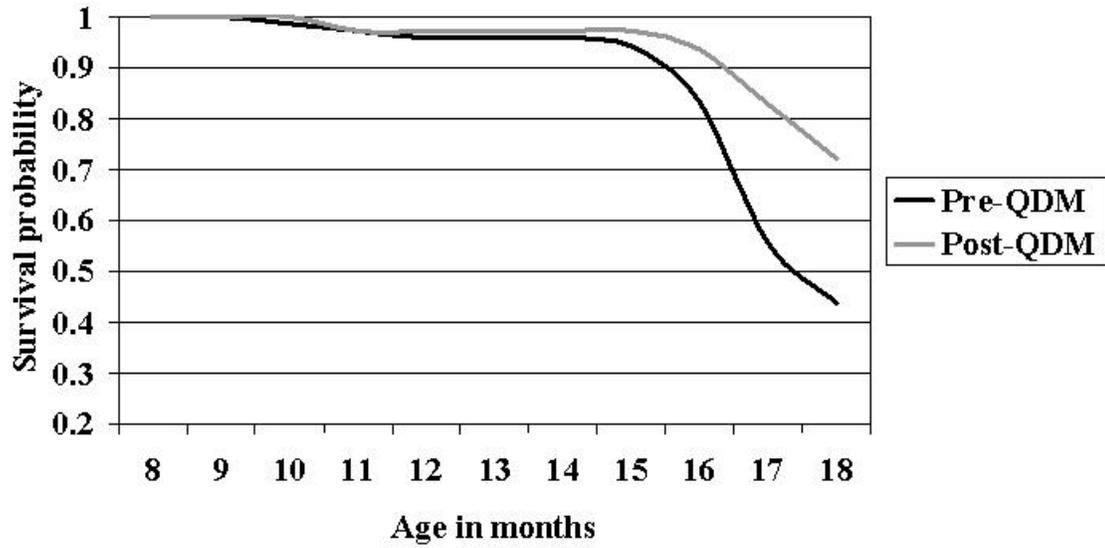


Figure 4: Pre-QDM (Rosenberry 1997) and post-QDM male survival probability from 8-18 months of age.

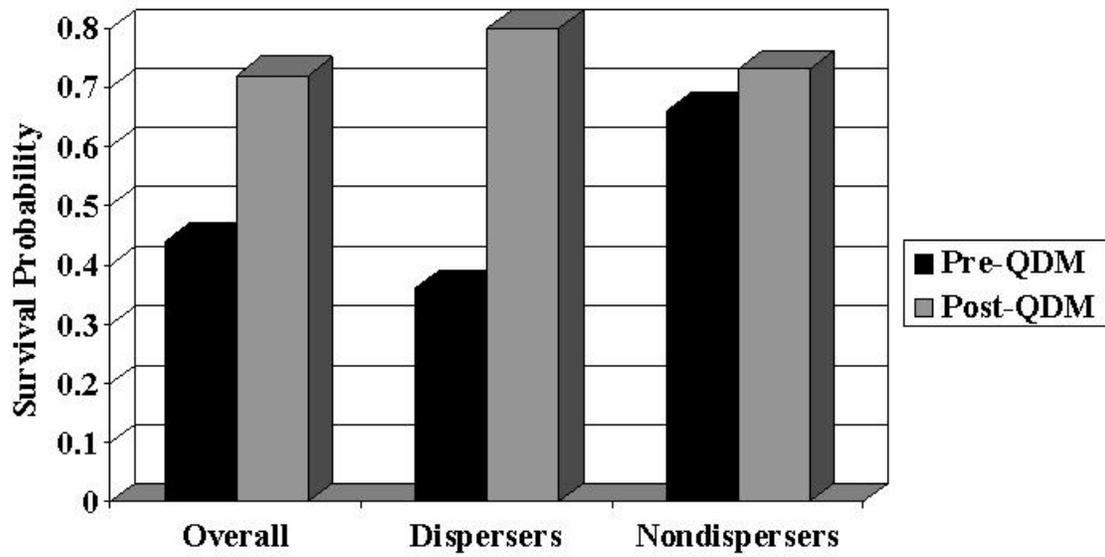


Figure 5: Pre-QDM (Rosenberry 1997) and post-QDM overall, disperser, and nondisperser male survival probability 8-18 months of age.

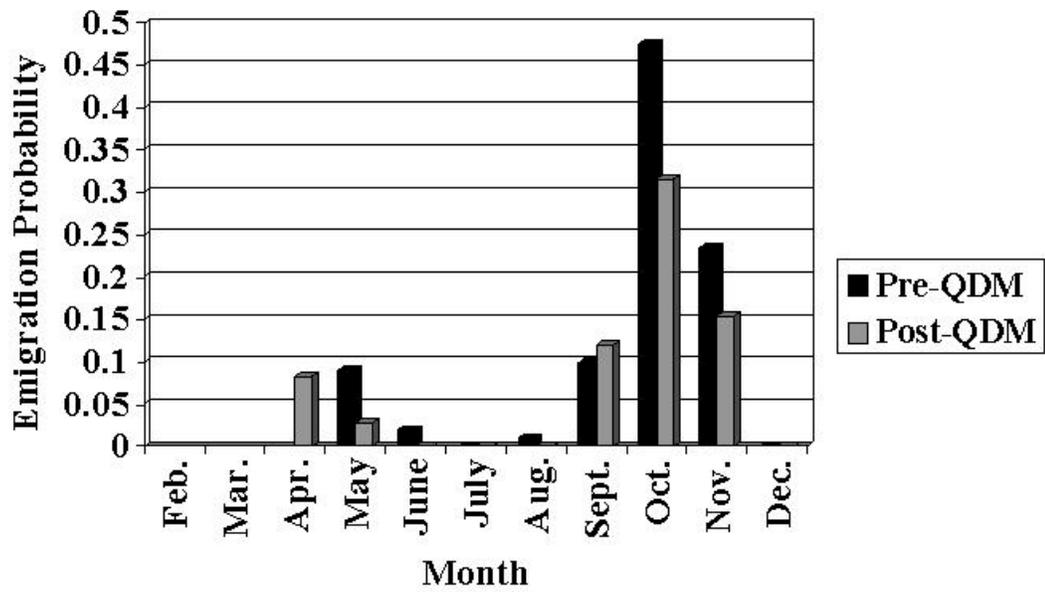


Figure 6: Pre-QDM (Rosenberry 1997) and post-QDM monthly yearling male dispersal probability.

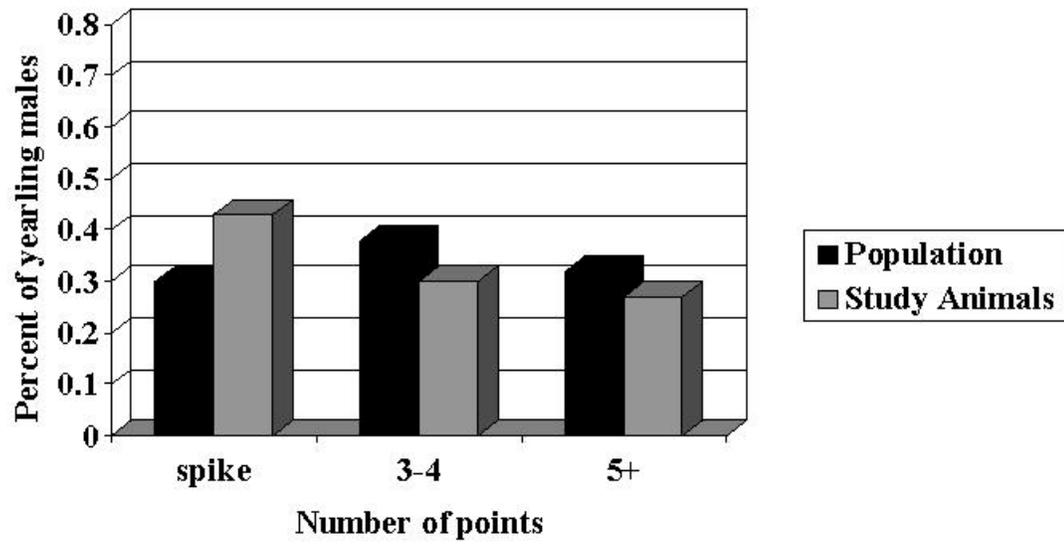


Figure 7: Post-QDM number of antler points observed in yearling male population and study animals.

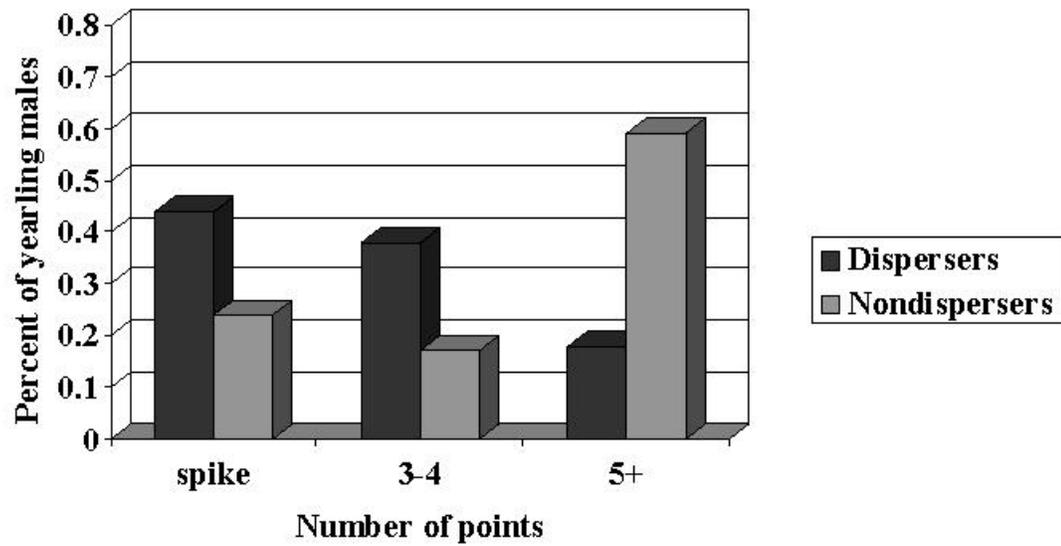


Figure 8: Disperser and nondisperser yearling male antler points pre-QDM (Rosenberry 1997).

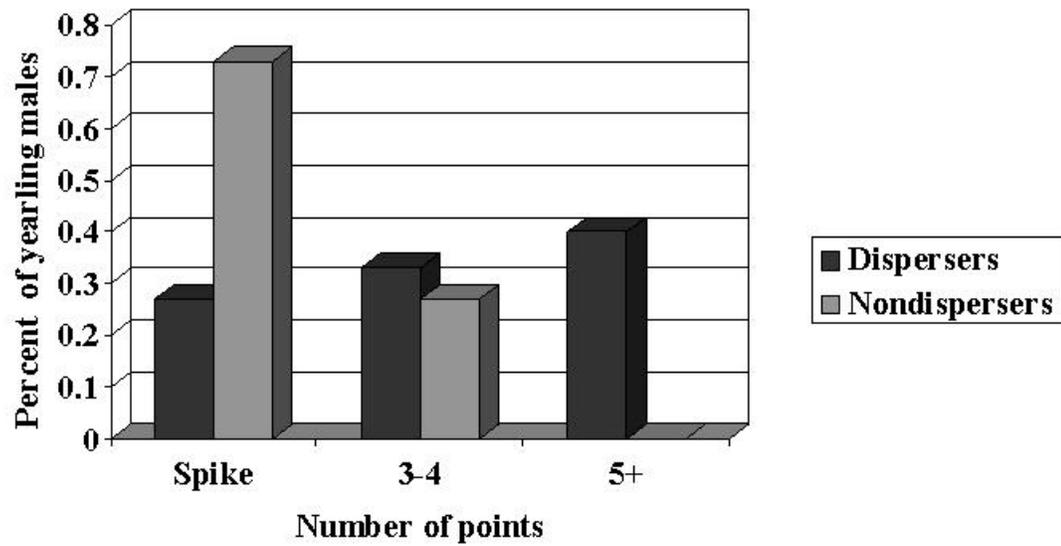


Figure 9: Disperser and nondisperser yearling male antler points post-QDM.

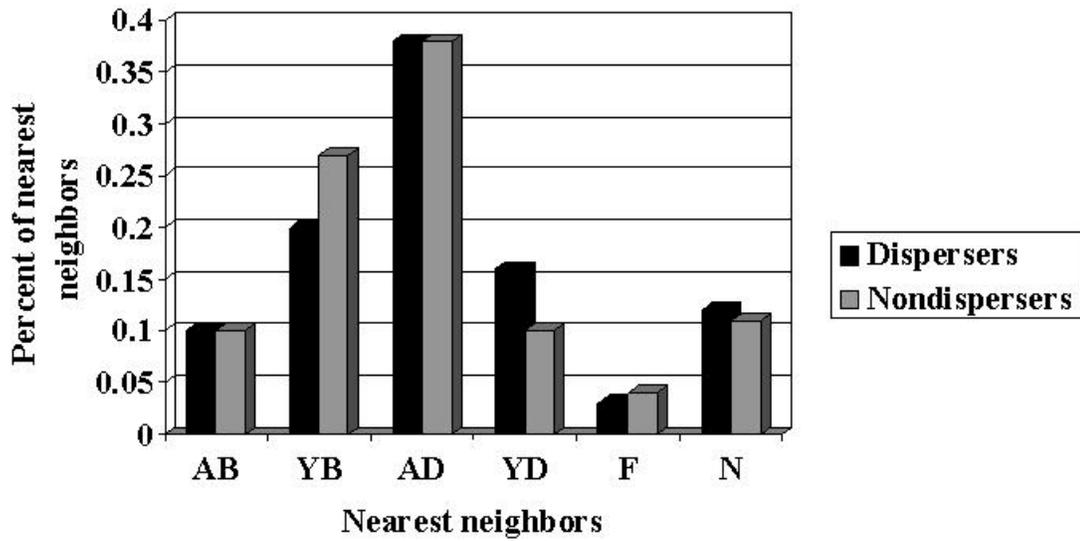


Figure 10: Post-QDM pre-breeding season disperser and nondisperser yearling male nearest neighbors.

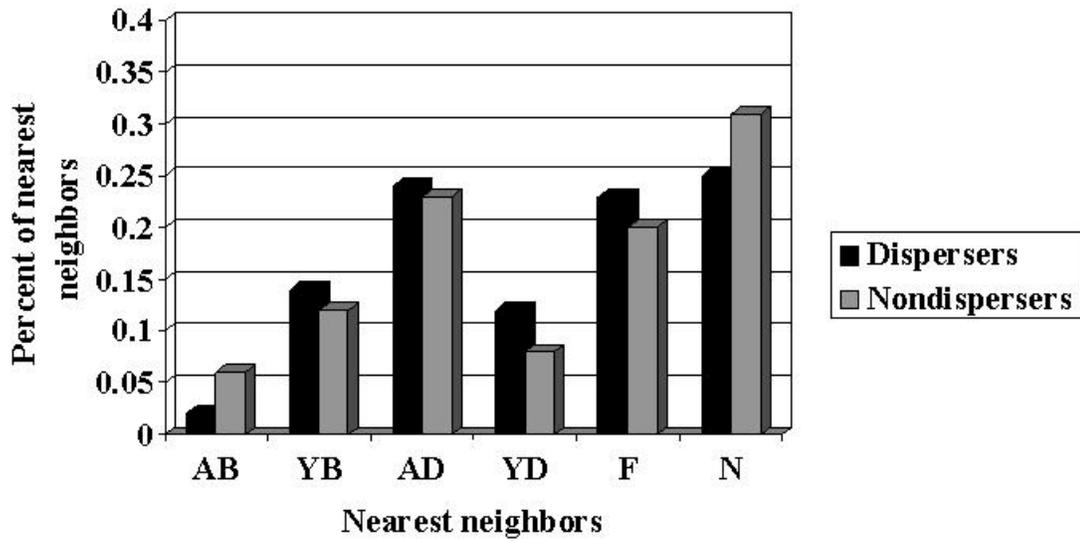


Figure 11: Post-QDM breeding season disperser and nondisperser yearling male nearest neighbors.

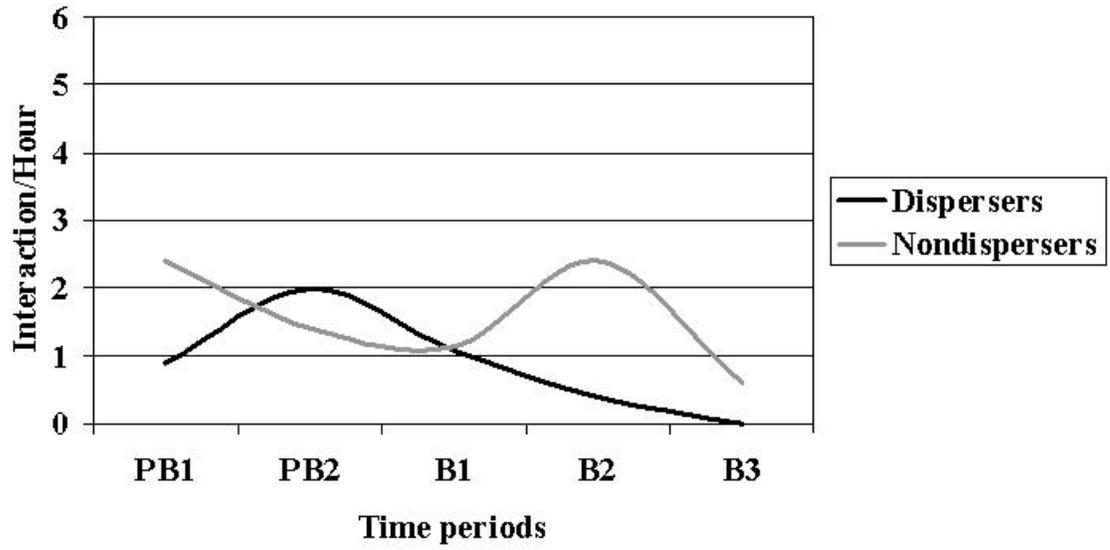


Figure 12: Post-QDM yearling male overall affiliative behaviors.

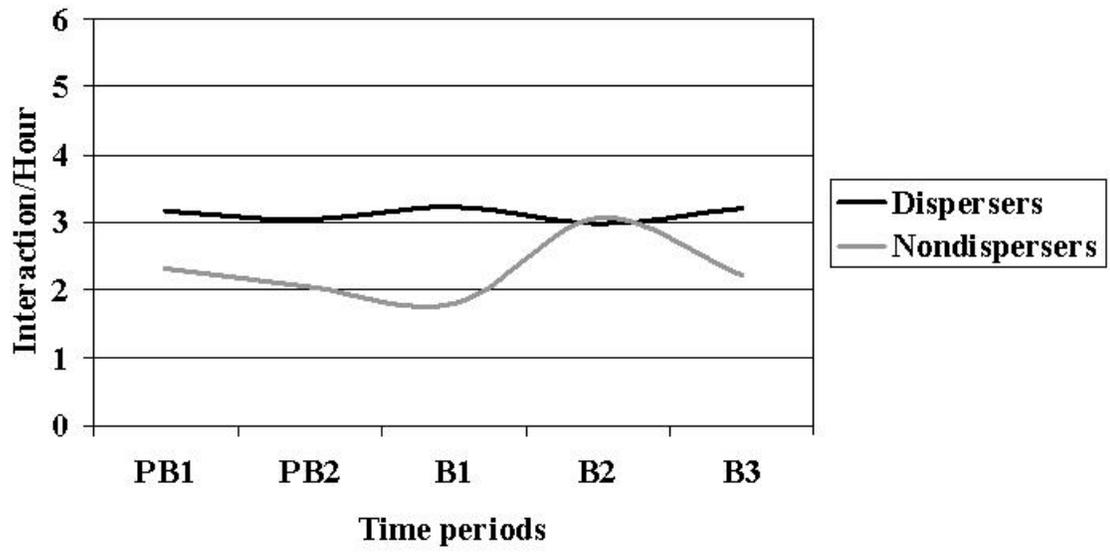


Figure 13: Post-QDM yearling male overall agonistic behaviors.

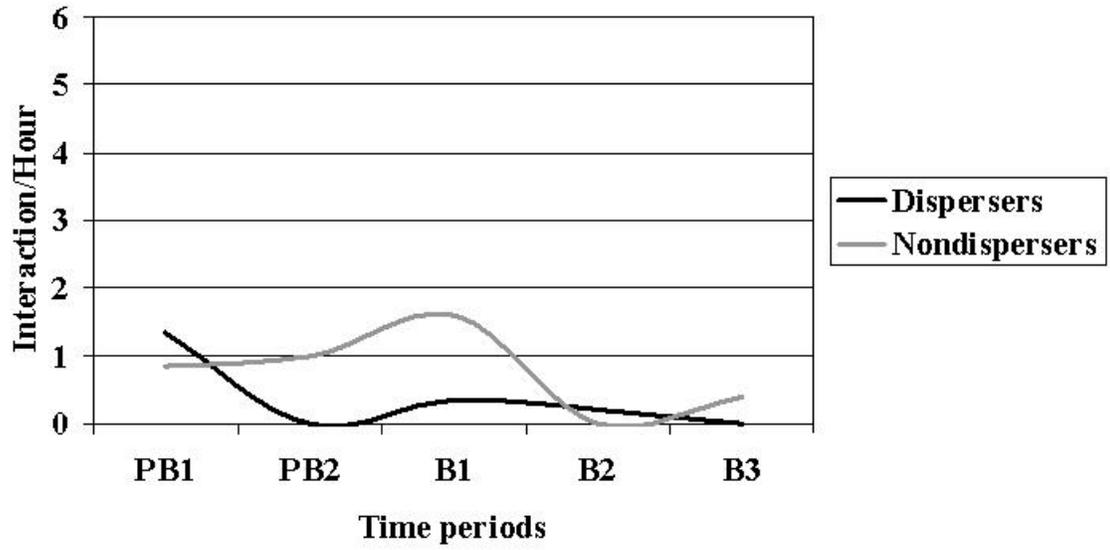


Figure 14: Pre-QDM yearling male agonistic behaviors with adult females (Rosenberry 1997).

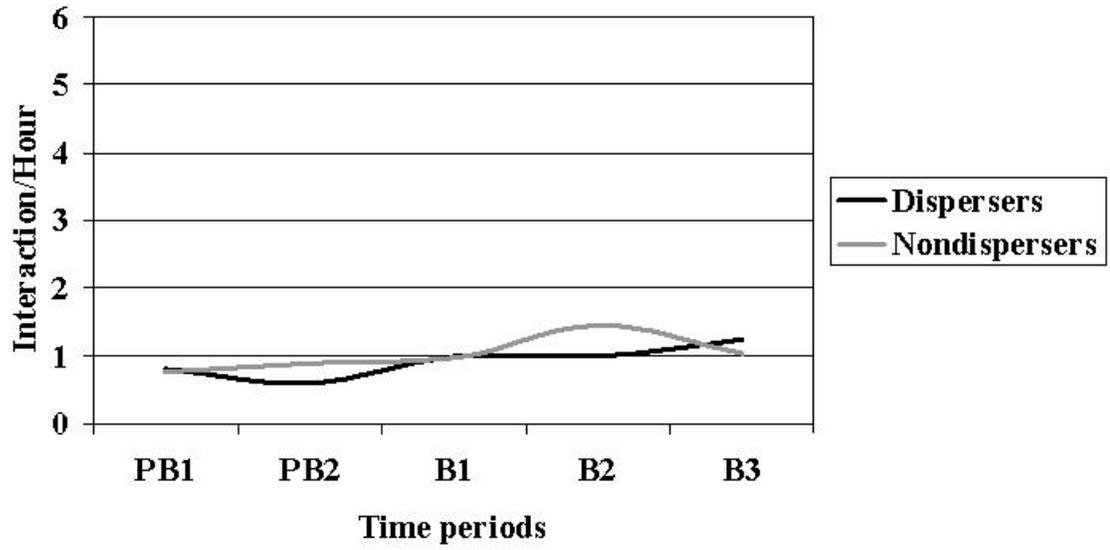


Figure 15: Post-QDM yearling male agonistic behaviors with adult females.

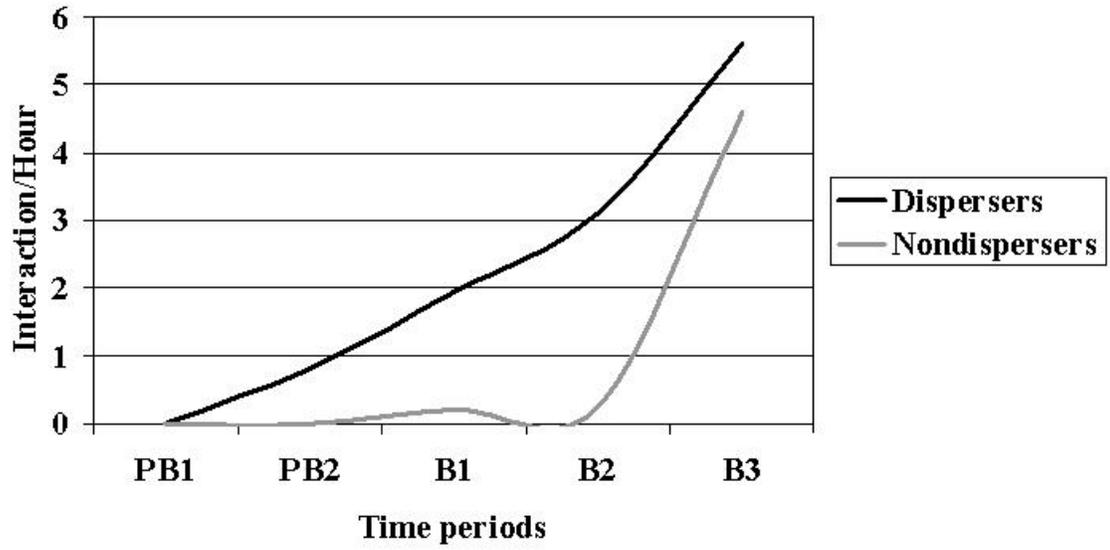


Figure 16: Pre-QDM overall yearling male breeding behaviors (Rosenberry 1997).

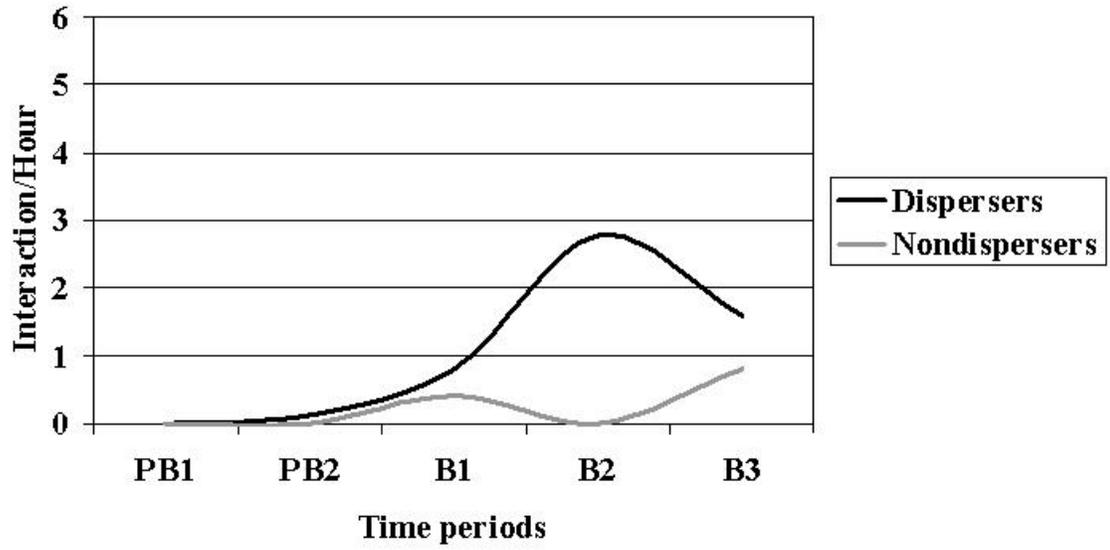


Figure 17: Post-QDM overall yearling male breeding behaviors.

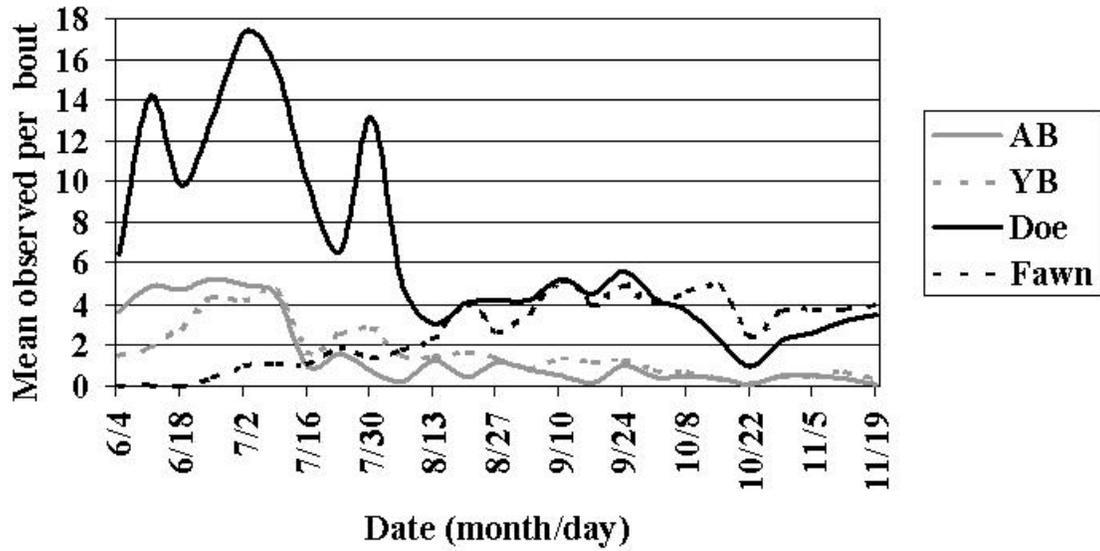


Figure 18: 2001 observability of adult bucks (AB), yearling bucks (YB), does, and fawns.

Observability is a function of the number of deer observed per 15 minute observation census conducted over an approximate 2 hour period at dusk.

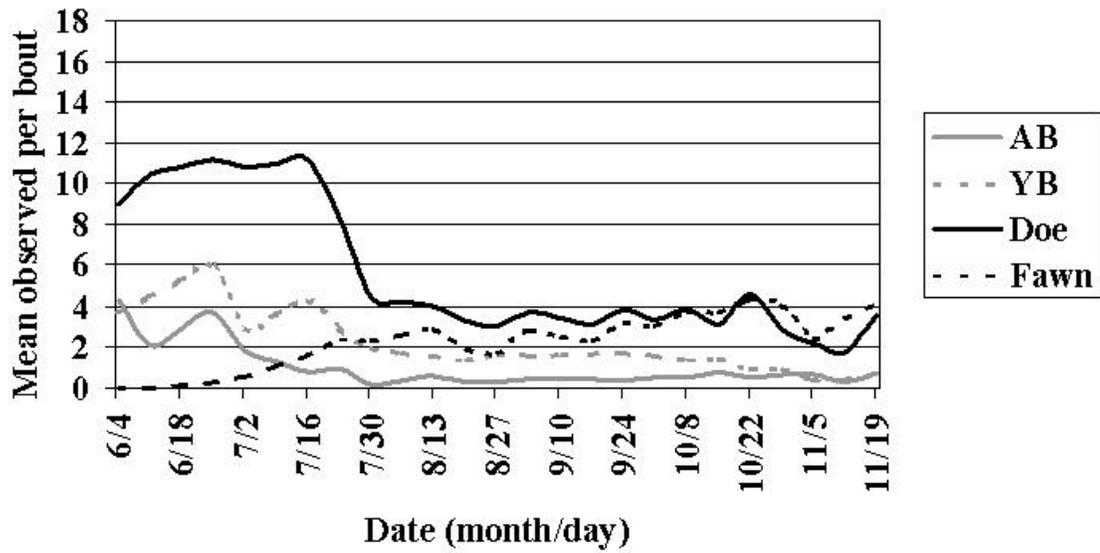


Figure 19: 2002 observability of adult bucks (AB), yearling bucks (YB), does, and fawns.

Observability is a function of the number of individual deer observed per 15 minute observation census conducted over an approximate 2 hour period at dusk.

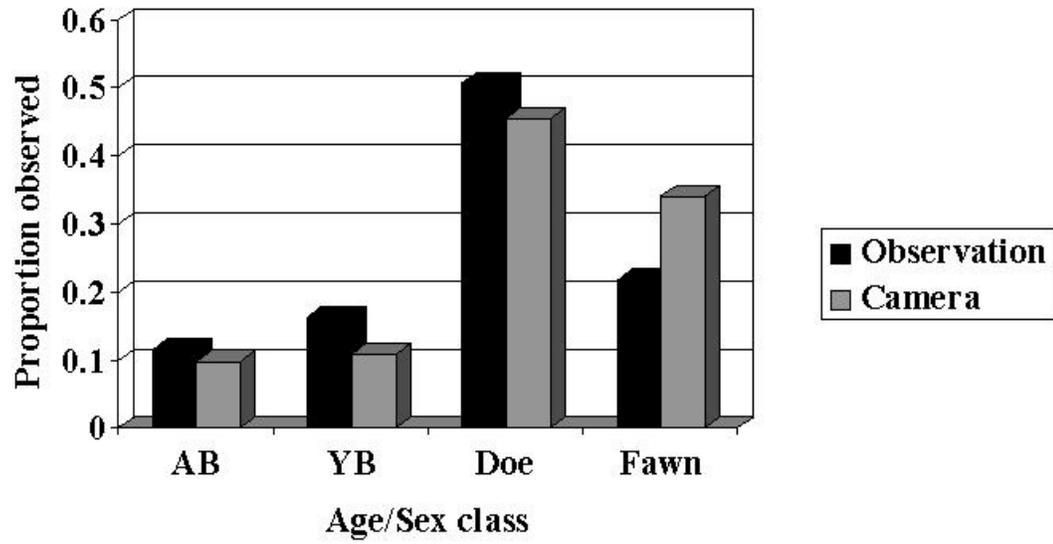


Figure 20: Infrared triggered camera census and observation census techniques comparison of proportion of age/sex classes observed.