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MOLECULAR EVALUATION OF THE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) MATING SYSTEM

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We used genetic-based paternity assignments from 3 diverse populations of white-tailed deer (*Odocoileus virginianus*) to evaluate the long-held assumption that male reproductive success in this species is highly skewed toward a small number of mature, dominant individuals. The study populations represented a range of adult sex ratios and male age structures. Male reproductive success was distributed among a large number of males in all populations, with no evidence for highly skewed access to mating for any individual male. Surprisingly, physically immature males (1.5 and 2.5 years of age) collectively fathered 30–33% of offspring in all populations, even where mature males were present. Ecological and behavioral variables appear to constrain the ability of individual males to monopolize access to females, resulting in a wider distribution of reproductive success than expected based on previous ecological and behavioral studies of white-tailed deer. Qualitative differences in the distribution of male reproductive success among study sites suggested that demographic attributes such as adult sex ratio and male age structure might influence the degree of competition for mates. Further study incorporating known-age cohorts or integrating movements and behavior is necessary for understanding the effects of population demographics as well as the physical and behavioral attributes that confer reproductive success in diverse populations of white-tailed deer.

Key words: mating system, *Odocoileus virginianus*, parentage, reproductive success, ungulate, white-tailed deer

Ungulate mating systems are typically polygynous, characterized by varying degrees of sexual dimorphism (Clutton-Brock 1989). Males compete intensely for mates and reproductive success is biased toward those individuals that most successfully control access to females. As a result, male reproductive success may be highly variable, with a few dominant, mature males fathering many offspring, whereas other males are unsuccessful (Clutton-Brock et al. 1988). Recent studies employing genetic markers have improved our understanding of ungulate mating systems, in some cases discrediting long-held assumptions (DeWoody 2005; Hughes 1998). Among the unexpected conclusions of genetic-based studies are that paternity assignments made using genetic markers can differ markedly from patterns of mating inferred from behavioral observations (e.g., Amos et al. 1995; Coltman et al. 1999; Gemmel et al. 2001; Pemberton et al. 1992). In addition, genetic studies have documented that social dominance alone may not guarantee reproductive success if opportunities to exercise dominance are limited (Worthington Wilmer et al. 1999), or if some males can be successful via alternative mating tactics (Hogg and Forbes 1997; Pemberton et al. 1999).

Although the white-tailed deer (*Odocoileus virginianus*) is the most abundant and widespread ungulate in North America (numbering ~26 million in the United States alone—Demarais et al. 2000), few genetic studies of mating behavior have appeared to date. Studies based on behavioral observations of mating have concluded that white-tailed deer form dominance hierarchies defined by age and body mass (Miller

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et al. 1987; Townsend and Bailey 1981). Male reproductive success has long been characterized as highly skewed, with a relatively small number of mature, dominant males siring each annual cohort (Hirth 1977; Marchinton and Hirth 1984; McCullough 1979). Sexual maturity occurs at 1.5 years of age and males are physically mature after 4 years of age (Sauer 1984; Strickland and Demarais 2000).

The conceptual model of a dominance-based, highly skewed mating system for white-tailed deer has recently been criticized because of an overreliance on behavioral observations and other circumstantial evidence (DeYoung 2004; DeYoung et al. 2006). Although a detailed genetic assessment of reproductive success in wild populations of white-tailed deer is lacking, recent studies of captive white-tailed deer (DeYoung et al. 2002, 2006) and a single enclosed population (Sorin 2004) have suggested that single males cannot monopolize breeding, resulting in a wider distribution of mating success among males (including physically immature males) than previously thought. However, the extent to which the results of studies involving captive and enclosed deer populations can be generalized to a wider range of populations awaits further evaluation.

A better knowledge of the mating system of white-tailed deer would be desirable from both basic and applied science perspectives, providing a means for understanding deer behavior and estimating basic population parameters. For instance, the distribution of male reproductive success within populations can provide insight into the evolution of mating systems and mating strategies (Fleischer 1996). Furthermore, the relationship between population demographic factors and male reproductive success is central to estimates of effective population size and population structure (Sugg and Chesser 1994). Finally, managers have alternately voiced concern over potential negative effects of male-biased harvest strategies on population fitness (Festa-Bianchet 2003; Harris et al. 2002; Rhodes and Smith 1992; Ryman et al. 1981), and proposed selective harvest strategies that attempt to manipulate the distribution of mating to improve population attributes (e.g., antler size—see Rollins 1998).

In this study, we used a panel of microsatellite DNA loci to assign paternity in 3 populations of white-tailed deer and evaluate the hypothesis of highly skewed male reproductive success. Long-term differences in harvest strategies across the study sites resulted in a range of adult sex ratios and male age structures. Our primary goal was to assess the distribution of male reproductive success in diverse populations of wild deer. A secondary goal was to perform a qualitative assessment of the effects of population demographics on the distribution of male reproductive success to lay ground for future studies of the effects of sex ratio and male age structure on male reproductive success.

MATERIALS AND METHODS

Study areas.—We chose 3 diverse populations of wild (noncaptive) white-tailed deer. The 22,000-ha Noxubee National Wildlife Refuge is located near Starkville in northeastern Mississippi. Public hunting is allowed on 17,500 ha and harvest pressure on males is intense. Sampling was concentrated on a ~3,200-ha portion of the refuge that had the greatest hunter use. The King Ranch is a large, private landholding (study population is part of an 80,000-ha contiguous property, managed under similar conditions) near Kingsville in southern Texas. Harvest of males was conservative and restricted to physically mature males. The Noble Foundation Wildlife Unit is a 1,200-ha research and management area near Allen in south-central Oklahoma. A 2.5-m electric fence was erected in 1992 to discourage trespass by humans (including illegal harvest) and facilitate management of the deer population due to the relatively small size of the area. The fence influences home ranges of deer, but is not a complete barrier to deer movements; deer trapped and marked on the area have been sighted or harvested on adjoining properties.

Sample collection.—We sampled deer on the Noxubee Refuge via hunter-harvest or special collection in cooperation with state and federal biologists. Deer harvested by public hunters must be brought to a central location for data collection; all harvested deer were sampled during 1998–2001. To increase the likelihood of assigning paternities, mature females were collected by permit each spring from 1999 to 2001 to obtain fetal samples from a known parent.

We sampled deer at the King Ranch via capture with a helicopter and net-gun (DeYoung 1988) or by harvest. Males were captured during October 1999–2001 and manually restrained. Pilots were instructed to capture the 1st antlered male they encountered. Varying numbers of fawns (aged 3–4 months) also were captured each year. During winter 2000, a separate study that required harvest of males in all age classes was conducted on a portion of the sampling area, which increased the sample of potential sires as well as known-age (1.5-year-old males) offspring. Mature females were collected during a special female-only hunting season in late January of 2000 and 2001 to obtain fetal samples from a known parent.

We captured deer on the Noble area using a drop-net (Schemnitz 1994) baited with shelled corn during January–April 1983–2002. Individuals were sedated using methods described in DeYoung et al. (2002) and marked with uniquely numbered plastic livestock ear tags for later recognition. Captured deer were sampled by taking ear tissue biopsies or blood. Ear biopsies were either frozen at −20°C or preserved in 70% ethanol. Blood was preserved in 0.5 M ethylenediaminetetraacetic acid, and stored at 4°C. Coordinated searches for cast antlers were begun in 1994 to provide an additional means of sampling males that eluded capture and harvest. Muscle or fetal tissue from all harvested individuals was frozen at −20°C. Field methods met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

DNA extraction and amplification.—We extracted total DNA from blood and tissue samples using either an organic solvent protocol or commercial kits as described previously (Anderson et al. 2002; DeYoung et al. 2003). Antler material was collected from the base of each cast antler using a 0.25-inch spade-tip drill bit; the resulting shavings were then processed using a commercial kit (Puregene DNA isolation kit; Gentra Systems Incorporated, Minneapolis, Minnesota). We amplified 17 DNA microsatellite loci from a panel optimized specifically for use in white-tailed deer (Anderson et al. 2002; DeYoung et al. 2003).

Locus properties.—We verified accuracy and repeatability of allele size calls based on blind comparisons using captive and wild deer with known parents (DeYoung et al. 2003). We estimated allelic richness (El Mousadik and Petit 1996), gene diversity (Nei 1987), and F_{IS} (Weir and Cockerham 1984) using the computer program FSTAT (Goudet 1995, 2001). The software also was used to perform tests for Hardy–Weinberg equilibrium (1,000 permutations of alleles among individuals) and linkage disequilibrium (8,000 permutations of genotypes among loci) within populations, adjusted using a Bonferroni correction to correct for multiple comparisons (Rice 1989).

Parentage assignment.—We placed sampled deer from each study area into groupings of potential sires (sexually mature males) or offspring cohorts (offspring with the same birth year from the same study area) according to their estimated ages using the tooth replacement and wear method (Dimmick and Pelton 1994; Severinghaus 1949). Cohorts and candidate sire pools were updated during each year to ensure that appropriate comparisons were made based on age at sexual maturity. Deer $\leq$ 1.5 years of age can be aged accurately, but the accuracy of estimated ages declines for age classes $>$ 2.5 years because of variability in tooth-wear patterns for individual deer (Gee et al. 2002). Therefore, potential sires were grouped into age classes 1.5, 2.5, and $\geq$3.5 years, a conservative method of accounting for known weaknesses in the Severinghaus (1949) method of ageing. With rare exceptions (e.g., isolated cases of early premolar tooth replacement in 1.5-year individuals trapped during spring), only individuals unambiguously aged $\leq$1.5 years when sampled were placed into offspring cohorts. Males sampled by cast antlers only were assigned the conservative age of $\geq$2.5 years and were considered only as potential sires.

We assigned parentage separately for each offspring cohort using the likelihood-ratio method in the computer program CERVUS 2.0 (Marshall et al. 1998; Slate et al. 2000). Simulations were performed to assess critical levels of the delta statistic (the difference in log-of-odds ratios between the most likely and 2nd most likely parents) that is used to determine the reliability of parentage assignments. The simulations to obtain critical values of delta were conducted for each offspring cohort separately (10,000 iterations for each cohort) using the empirically observed allele frequencies and proportion of loci typed, and an estimated typing error rate of 1% based on known parent–offspring comparisons (DeYoung et al. 2003). Parentage was assigned at a minimum 80% confidence threshold, the critical level of the delta statistic derived from simulations in which the simulated parent was correctly assigned parentage 4 out of 5 times. Parentage assignments at the 80% threshold are commonly presented in the literature (Marshall et al. 1998; Slate et al. 2000) where no known parents are available under the rationale that any errors are likely to be random.

Indices of population demographics.—Each of the study populations had different demographic characteristics (male age structure and sex ratio) as a result of long-term differences in harvest management, thus permitting a qualitative evaluation of the effects of population demographics on male reproductive success. We indexed adult sex ratio at the Noxubee Refuge using nocturnal spotlight surveys during late winter throughout the study period. We traversed a 20-km transect representative of the collection area on at least 3 separate occasions during each year of the study. Male age structure was estimated from harvest records. Harvest pressure for both sexes at Noxubee is relatively intense and many hunters take the 1st legal deer they encounter. However, the harvest distribution at Noxubee is not likely to provide an unbiased estimate of male age structure because of a statewide regulation that began in 1995 stipulating that legal bucks must have $\geq$4 total antler points. As a result, the harvest proportions during the study period would underestimate the number of 1.5-year males in the population. Harvest records from Noxubee during 1989–1994 indicated that 73% of 1.5-year males had $<$4 antler points and would not be eligible for harvest. Therefore, the proportion of 1.5-year males in the population during the study period was adjusted to account for the 73% of 1.5-year males ineligible for harvest.

We estimated adult sex ratios at King Ranch during aerial line transect surveys performed from helicopters during each fall (DeYoung et al. 1989). Male age structure was estimated from capture records, assuming males were captured without an age bias because of the nonselective nature of the capture criteria (i.e., the 1st antlered male encountered was captured during each sortie). Nocturnal ground-based, incomplete line transect surveys (Lancia et al. 1994) using spotlights were performed each fall throughout the entire study period and served as an index to sex ratio and age structure (Gee et al. 1994). We also used infrared still and video cameras (Jacobson et al. 1997) to index adult sex ratio and age structure of the Noble population during late winter. A large group of marked deer was maintained during the study period (approximately 40–60% of the total population) and served as a subpopulation of known sex and age composition. The use of 2 separate methods allowed verification of estimates and correction for known weaknesses of each technique (e.g., proportion of fawns can be underestimated during fall spotlight surveys, whereas females are undercounted at camera stations due to social interactions with adult males).

RESULTS

Locus properties.—We genotyped 1,219 individuals from the 3 populations: 439, 502, and 278 from King Ranch, Noble, and Noxubee, respectively. All populations had high and similar levels of allelic richness and gene diversity; F_{IS} values were generally low and similar (Table 1). More than 90% of

Table 1.—Population and cohort descriptive statistics and paternity assignment based on allele frequencies at 17 DNA microsatellite loci for 3 diverse populations of wild white-tailed deer (*Odocoileus virginianus*).

Area	Allelic richness (*SD*)	Gene diversity (*SD*)	F_{IS} (*SD*)	Cohort birth year	*n*	Paternities assigned (%)[a]
Noxubee National Wildlife Refuge	10.4 (5.5)	0.73 (0.20)	0.043 (0.08)			
				1998	42	5 (12)
				1999	53	7 (13)
				2000	48	6 (12.5)
				2001	27	2 (7)
Noble Foundation Wildlife Unit	9.4 (4.9)	0.72 (0.19)	0.059 (0.09)			
				1991	17	1 (6)
				1992	18	5 (28)
				1993	36	11 (31)
				1994	29	6 (21)
				1995	41	20 (49)
				1996	36	20 (56)
				1997	31	19 (61)
				1998	22	16 (73)
				1999	21	11 (52)
				2000	37	24 (65)
				2001	24	21 (87.5)
King Ranch	8.4 (4.3)	0.73 (0.15)	0.042 (0.09)[b]			
				1998	23	0 (0)
				1999	61	14 (23)
				2000	82	31 (38)
				2001	71	25 (35)

[a] Percentage of sampled offspring for which paternity was assigned.

[b] 95% confidence interval includes 0.

individuals had complete genotypes (King Ranch: 90%; Noble: 92%; Noxubee: 94%). Permutation tests revealed no significant linkage disequilibrium or deviations from Hardy–Weinberg expectations after Bonferroni corrections.

Parentage assignment.—The microsatellite markers were highly polymorphic in all 3 populations, with estimated exclusion probabilities >0.99 both with and without genetic information from a known parent. All parentage assignments were made with ≤2 mismatching loci. The 439 deer from the King Ranch included 237 fetuses, fawns, and yearlings that could be placed into birth cohorts during 1998–2001 (92 with a known parent; Table 1). Forty-six males fathered 70 offspring (29.5% of sampled offspring). Mean reproductive success was low for individual successful males ($\bar{X}$ = 1.6, var = 1.03), but most offspring (70%) were sired by males ≥3.5 years of age. Males in the 1.5- and 2.5-year age classes sired 14% and 16% of offspring, respectively (Fig. 1). Thirty-five of the 70 paternity assignments met the simulation criteria for 95% confidence.

The 502 deer sampled at the Noble area included 312 fawns and yearlings that could be placed into cohorts for birth years 1991–2001 (Table 1). Sixty-one males fathered 154 fawns (49% of sampled offspring). Similar to King Ranch, mean individual reproductive success was low ($\bar{X}$ = 2.5, var = 6.22), and males in older age classes were most successful. Males ≥3.5 years sired 67% of our sample of fawns born on the Noble area, whereas males in the 1.5- and 2.5-year age classes sired 11% and 22% of fawns, respectively (Fig. 1). Ninety-five of the 154 paternity assignments met the simulation criteria for 95% confidence.

The 278 Noxubee samples included 170 fetuses, fawns, and yearlings in birth cohorts 1998–2001 (76 with a known parent; Table 1). Parentage assignment success was low, with sires assigned for only 20 offspring (16 males; 12% of sampled offspring). Eleven of the 20 paternity assignments met simulation criteria for 95% confidence. Males aged 1.5, 2.5, and ≥3.5 years sired 6 (32%) of 19, 7 (37%) of 19, and 6 (32%) of 19 offspring, respectively (Fig. 1). An age estimate was not recorded for 1 sire, but it is likely that this individual was >2.5 years of age based on the distribution of body weight and antler measurements from the Noxubee harvest during 1989–2001.

Population demographics.—Sex ratios and male age structure in the 3 study populations varied with harvest strategy of males. Adult sex ratio at the King Ranch was about 2.7 females per male. Male age structure was diverse and consisted primarily of mature males (1.5 years: 23%; 2.5 years: 19%; ≥3.5 years: 57%). Adult sex ratio on the Noble area varied during the study, but was ≤2.5 females per male. Males in age classes 1.5, 2.5, and ≥3.5 years comprised 44%, 26%, and 30% of the male population, respectively. The Noxubee population was highly skewed toward females (postharvest sex ratio: ≥7 females per male). Males in age classes 1.5, 2.5, and ≥3.5 years accounted for roughly equal portions of the harvest during 1998–2000: 34%, 30%, and 37%, respectively. Using the pre-1995 harvest data to adjust for hunter selection bias due to the ''4-point'' harvest regulation, we estimate that approximately 80% of Noxubee males were <3.5 years of age (1.5 years: 64%; 2.5 years: 17%; ≥3.5 years: 19%).

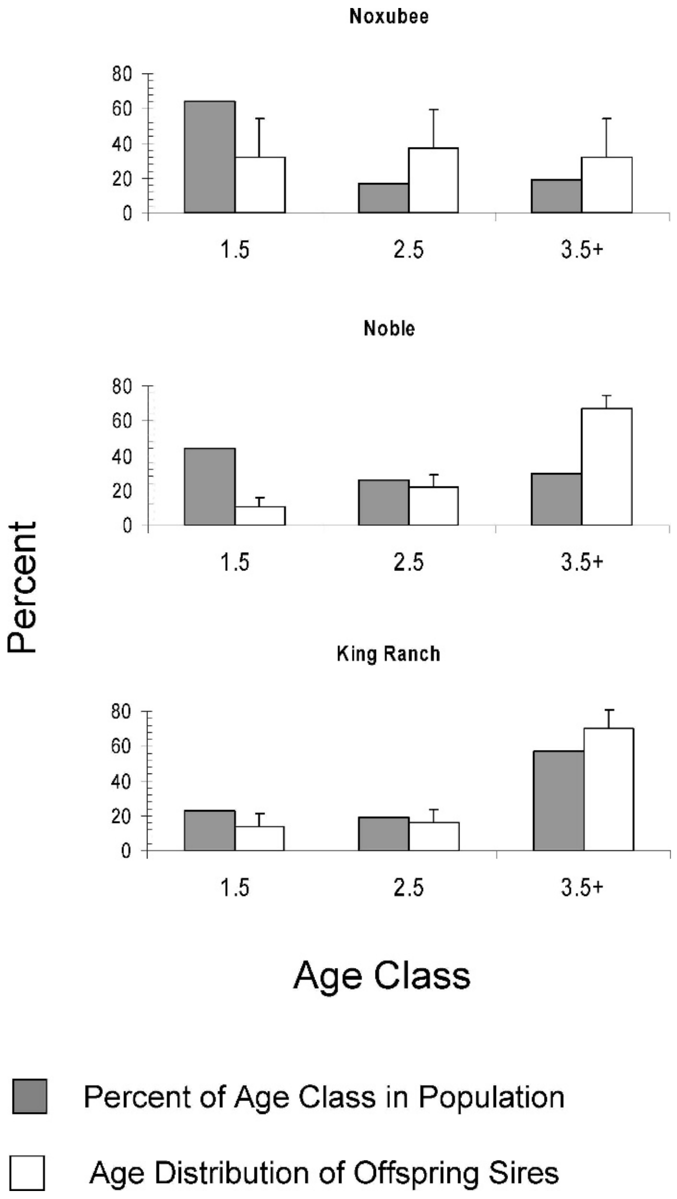

FIG. 1.—Male age structure and distribution of male reproductive success by age class for 3 populations of white-tailed deer (*Odocoileus virginianus*) sampled during 1992–2001. Reproductive success was estimated based on paternity assignment using 17 microsatellite loci. Bars indicate 95% bound on error of estimation, where more samples reflect greater confidence in the stated proportions.

DISCUSSION

Overall, paternity assignments clearly indicated that breeding was apportioned among males in all age classes in all populations. The distribution of mating also was consistent across the temporal scale of our study (4–11 annual cohorts) for all 3 populations; we detected no evidence that 1 or a few males monopolized breeding. Trends in parentage assignment success further support a wide distribution of mating. For instance, several years of intense efforts were required before paternity could be assigned to a reasonable number of fawns in an annual cohort (e.g., Table 1). This occurred despite the fact that we made a concentrated effort to include a large proportion of mature males in our initial samples of candidate males on each area. Our results suggest that a wide distribution of mating among individuals and age classes, 1st observed in studies of genetic paternity in captive white-tailed deer (DeYoung et al. 2002, 2006) and an enclosed unharvested population (Sorin 2004), might be common in free-ranging populations of white-tailed deer.

Collectively, studies employing genetic parentage in white-tailed deer are consistent in detecting widespread paternity across a range of demographic conditions, harvest regimes, temporal sampling, and habitat types. The pattern of male mating derived from genetic parentage, especially the proportion of offspring sired by young males, is quite different from those expected based on previous ecological and behavioral studies of white-tailed deer (see Hirth 1977; Marchinton and Hirth 1984; McCullough 1979), which assumed that most offspring were sired by a small number of dominant males. The observed distribution of mating in white-tailed deer also differs widely from highly polygynous ungulates, which often display harem or lek mating systems. For instance, the most successful male red deer (*Cervus elaphus*) in a Scottish population may have sired 86 surviving offspring during a lifetime (Pemberton et al. 1992), whereas 3% of males gained 73% of copulations in a group of European fallow deer (*Dama dama*—McElligot and Hayden 2000). In each case, only a few mature males sired offspring, whereas young males and many mature males were unsuccessful.

The genetic parentage results in white-tailed deer populations raise at least 2 questions. Why is reproductive success apportioned among a larger number of males than expected for a dominance-based breeding hierarchy? Why do young males breed in all populations and why is their success not limited to situations where they possess numerical superiority? Studies using genetic-based paternity assignment in a variety of taxa have demonstrated patterns of mating that differ from those based on observation because some individuals and copulations are more easily observed than others. This is apparently the case for white-tailed deer, a species that prefers dense habitats for escape cover (Demarais et al. 2000; Hirth 1977), thus making the acquisition of actual behavioral evidence of copulations difficult to obtain. In fact, the most intensive behavioral study of free-ranging white-tailed deer recorded only 4 copulations in 3 years observation (Hirth 1977).

The dense cover and patchy distribution of resources in white-tailed deer habitats inhibits the formation and maintenance of large groups (Demarais et al. 2000), ruling out lekking, territoriality, or harem defense as viable male mating strategies (Clutton-Brock 1989). Male mating tactics consist of roaming widely in search of individual estrous females, with males spending up to 24 hours ‘‘tending’’ each receptive female (Hirth 1977). Most conceptions occur in a relatively short period of time (2–4 weeks in temperate populations—Marchinton and Hirth 1984). The overall spatial dispersion of females within populations combined with temporal synchrony of estrus would limit the number of estrous females an individual male can locate and breed, allowing more males access to mating opportunities (e.g., Say et al. 2001). Finally, there is evidence for female promiscuity in white-tailed deer (DeYoung et al. 2002, 2006; Sorin 2004), which may further enhance chances of successful mating by males of all age classes (e.g., Pemberton et al. 1999).

In highly polygynous species such as red deer, contest competition (fighting) among males is critical to male mating success (Clutton-Brock et al. 1988) such that only mature, large-antlered males in good physical condition are able to defend harems and gain access to females (Kruuk et al. 2000). As a result, young males do not challenge mature males for breeding access, deferring reproductive effort until physical maturity to invest in skeletal growth (Yoccoz et al. 2002). In contrast, a wide distribution of breeding among male individuals and age classes suggests that contest competition may be less important to the reproductive success of individual male white-tailed deer. Some level of reproductive investment by physically immature males may be favored if fighting is not necessary for gaining and defending mates. Young or subdominant males may successfully gain fertilizations through investing in mate-searching or employ alternative strategies that do not rely on dominance. Early investment in reproductive effort may be partly tied to a life-history strategy, because white-tailed deer lie more toward the *r* side of the *r*-*K* life-history continuum than many other species of large mammals, as evidenced by a comparatively early age of sexual maturity and regular production of twin offspring (Geist 1998). Thus, there may be less advantage for young male white-tailed deer to defer reproduction in the current year for future gain.

Ecological and behavioral variables appear to limit the ability of individual male white-tailed deer to monopolize access to >1 female at a time. If this reasoning is correct, opportunities to exercise dominance would be limited to interactions over individual estrous females (e.g., Worthington Wilmer et al. 1999), and some males might successfully employ alternative tactics that do not rely on dominance (e.g., Hogg and Forbs 1997; Pemberton et al. 1999). Thus, individuals in a tending bond mating system could face an upper limit in terms of mating opportunities relative to the opportunities available to a dominant male in a harem or lek mating system.

We observed differences among populations in adult sex ratios and male age structure consistent with the number and age classes of males harvested, permitting a qualitative evaluation of how these demographic factors might affect male reproductive success. The King Ranch and Noble sites had similar sex ratios, yet differed in male age structure. Despite an almost 2-fold difference in the proportion of mature males (57% versus 30%), the reproductive success of males sampled in this age class was similar in both populations (King Ranch: 70%, Noble: 67%). Although the reproductive success of individual males on both areas was low, older males appeared consistently more successful than young males in situations where sex ratios were relatively balanced. We also observed a qualitative increase in the variance of reproductive success between Noble and King Ranch, which might reflect a difference in the degree of competition for mates (note that we refer to statistical variance of the sample here, not variance considering both successful and unsuccessful males, as in Brown [1988]). We are reluctant to present a direct comparison between study areas because of differences in offspring sample composition; 40% of the King Ranch offspring samples were composed of fetuses in utero, whereas estimates for Noble were based on single fawns sampled at ≥4 months of age, after peak fawn mortality. Nevertheless, greater competition for mates at King Ranch would be logical considering the difference in male age structure between the 2 areas.

Studies of unexploited populations of large mammals suggest 2 possible outcomes when adult sex ratios are skewed in favor of females: more uniform reproductive success for males of all age classes (e.g., Pemberton et al. 1999); or an overall decrease in competition for mates among mature males only and a failure of young males to obtain fertilizations (e.g., Clutton-Brock et al. 1997). Although paternity was established for fewer males at Noxubee, the overall trend observed is compatible with an increase in mating opportunities for all age classes. Reproductive success was distributed evenly among age classes, with no evidence that reproductive success was highly skewed toward a few individual males. In fact, our limited success in assigning paternity at Noxubee might be attributed in part to a wide distribution of breeding coupled with our method of obtaining samples. Unlike the other 2 areas, all samples of candidate sires at Noxubee were taken through harvest. When paternity is widespread and life span of males is short due to intense harvest pressure, it becomes difficult to maintain a large sample of candidate males because males are continually removed from the breeding population as they are sampled. As a result, the percentage of potential sires sampled each year reaches a plateau rather than continually increasing as additional live males are sampled. Our data set did not permit a more detailed breakdown of reproductive success within and among age classes of males due to sample size within years and the limitations of the tooth-wear ageing technique (see Gee et al. 2002). For instance, our grouping of all mature males into a single category is a conservative means to address uncertainty in ageing, but sacrifices the ability to determine the relative reproductive success of males within-class (e.g., prime-aged males versus senescent males). Detailed, long-term data on reproductive success of known-age male cohorts could reveal much about factors conducive to individual reproductive success in white-tailed deer.

The effects of demographic factors such as adult sex ratio and male age structure on male reproductive success have yet to be firmly established. However, physically immature males in our study invested in reproductive effort over a range of demographic conditions and collectively sired a large proportion of offspring. Altering demographic parameters could affect the distribution of male reproductive success among age classes (and perhaps individuals) by altering the competitive environment for mates. Further study incorporating behavioral or movement data in conjunction with genetic parentage is necessary to reveal the suite of successful mating tactics employed by males of differing age and dominance status.

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