Evaluation of Reproductive Behavior in White-tailed Deer through Genetic Parentage Analysis

by

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Abstract

Few studies have utilized genetic technology to examine reproductive behavior in white-tailed deer through parentage analysis, resulting in gaps in knowledge of reproductive behavior in white-tailed deer. This study examined relationships between reproductive success in male white-tailed deer and body size, age, and antler characteristics, age-related mate choice, and inbreeding avoidance using genetic parentage assignment. Between December 2007 and August 2010, 115 deer from inside a 174-ha high-fence facility in Alabama were sampled and genotyped. Fifty-four paternities and 48 maternities were assigned using the program CERVUS. No relationship was detected between male reproductive success, body size, and antler characteristics. However, prime-aged males were more likely to breed and sired more offspring on average than younger males. Three cases of multiple paternity were observed, including the first reported triplet multiple paternity with 3 different sires. Evidence of age-related mate choice was identified, but no evidence of inbreeding avoidance behaviors was found.

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I. Literature Review of White-Tailed Deer Reproductive Behavior

Male White-Tailed Deer Reproductive Success

Age

Age is a trait that tends to be associated positively with male reproductive success. With age comes sexual, physical, and social maturity, all important for males to be reproductively competitive. Multiple studies on white-tailed deer have documented greater reproductive success in prime-aged bucks (>3.5 years of age) than in yearling bucks (Jacobson 1992, Miller and Ozoga 1997, Sorin 2004, DeYoung et al. 2009a). Typically, few yearlings sire offspring in populations with a significant population of mature bucks (Sorin 2004, DeYoung et al. 2009a). In a penned study, DeYoung et al. (2006) found that 64 - 100% of fawns from pens where dominance did not change were sired by the dominant males who were all older than 1.5 years of age and usually the oldest male in the pen. Deyoung et al. (2009a) also studied 3 free-ranging populations. Two of the populations had sex ratios of ≤3:1 does to each buck and about 30 - 50% of the bucks were ≥3.5 years of age. These populations had approximately 70% of the sampled fawns sired by males 3.5 years of age and older. The third population was under greater hunting pressure and had a buck-to-doe ratio of <1:7 with approximately 80% of the males <3.5 years of age. Though this population had a very low parentage assignment rate of 12%, DeYoung et al. (2009a) found that males 3.5 years of age and older sired 32% of offspring, the same proportion as yearlings. The lack of mature bucks in the third population meant that yearlings were able to sire many more offspring than in the two populations where 30 - 50% of bucks were ≥3.5 years of age. Sorin (2004) conducted a similar study with a simulated free-ranging population with a buck-to-doe ratio of 1:2 where 41.2% of males (excluding fawns) were >3 years of age. Males 3.5 years of age and older sired 85% of sampled offspring and were the most successful individually with 86% of males ≥3.5 years of age siring offspring compared to just 18% of yearlings and 50% of 2.5 year-olds. This study also found that the number of females a male successfully mated with and the number of offspring a male fathered were associated with male age, though the correlation was not significant when yearlings were removed from the analysis. Studies on other cervid and polygynous species have also found that older males are the most reproductively successful. For example, prime-aged (7 - 10 years of age), dominant, male red deer (*Cervus elaphus*) were assigned paternity to 56% of sampled offspring, and it was suggested that other unsampled dominant males fathered most of the 34% of offspring whose paternity could not be assigned to any sampled males (Pemberton et al. 1992). Young males were hypothesized to sire very few offspring compared to mature, dominant males.

Older males likely have greater reproductive success because they are generally dominant over young males. In many species, age is an important factor in dominance because males must reach sexual, physical, and social maturity to compete for dominance. Additionally, body size increases with age and ornamentation used as a secondary sexual characteristic, like antlers, becomes more prominent and more ornate as males become older. Age also brings an increase in reproductive hormones, such as testosterone, that tend to increase male aggressiveness (Miller et al. 1987, Bubenik and Schams 1986). Experience gained with age also plays an important role in being successful in acquiring dominance. For example, prime-aged white-tailed bucks (>3.5 years of age), the most reproductively successful age group (DeYoung et al. 2009a), were found to be dominant over males 2.5 years and younger in penned studies (Townsend and Bailey 1981, DeYoung et al. 2006). More specifically, Townsend and Bailey (1981) observed a penned population of white-tailed deer over a 2 year period and created a social ranking of all deer by the outcome of encounters. Adult males were typically dominant over yearling males and were always dominant over male fawns. In a smaller scale study, DeYoung et al. (2006) found that the oldest male in the pen tended to be dominant at the beginning of the study. In two of the three pens with a 3.5 year-old male and a 5.5+ year-old male present, the 3.5 year-old male was initially subordinate, but became dominant over the course of the study, while in the third pen, the 3.5 year-old buck was dominant from the beginning. There were also 3 pens with 2 yearlings and one 2.5 year-old male each where the 2.5 year-old males were always dominant over the yearlings. For all 6 pens, the dominant males sired the greatest number of offspring; in the two pens where dominance changed, both dominant males sired more offspring than most subordinate males sired in the other pens. Male red deer on the Isle of Rhum also demonstrate relationships between age, dominance, and reproductive success (Clutton-Brock et al. 1979). Reproductive success and fighting success (an indicator of dominance) both peak at 7 - 10 years when stags are mature. The study also found that age was a significant factor in determining fighting success, which strongly influenced reproductive success. Males 7 - 10 years of age were the most victorious in fights and were able to hold harems with a greater number of females (Clutton-Brock et al. 1979), making age an accurate indicator of reproductive success in red deer (Pemberton et al. 1992). For fallow deer bucks (*Dama dama*), older males were also the more dominant age group, and dominance rank is the most influential factor in male reproductive behavior and success (Komers et al. 1997).

Polygynous grey seals (*Halichoerus grypus*) also exhibit an increase in reproductive success as dominance rank increases (Godsell 1991). As male grey seal age increases, body size also increases, though physically and socially mature males had no correlation between weight and tenure (a measure of dominance) if age was removed from the model. Similarly, there was no correlation between weight and rates of copulation without age as a factor in the model, so the relationship between weight and mating success seems likely only through the relationship between age and weight (Godsell 1991).

Another reason older bucks are more successful breeders than younger males could be that older males are more efficient breeders. In populations of white-tailed deer that are dominated by yearling bucks, breeding can peak 2-3 weeks later than in populations dominated by older males because older males may be better able to successfully mate with females during the first estrous cycle (Ozoga and Verme 1985, Jacobson 1992, Miller and Ozoga 1997). When yearlings dominate a population, the breeding period is also typically longer, later, and can vary more in length of time (Ozoga and Verme 1985, Miller and Ozoga 1997). During the breeding period, yearling bucks are more aggressive and shed their velvet later than mature bucks which makes them less efficient at acquiring breeding opportunities (Ozoga and Verme 1985).

Older males put greater effort into reproduction during the peak of breeding, increasing their reproductive success and suppressing the efforts of younger males. Ozoga and Verme (1985) found that yearling bucks were less active during the breeding season and exhibited less courtship behavior. Additionally, yearling reproductive effort is suppressed because older males are able to breed does during the first estrous cycle, dominating available mating opportunities and shortening the breeding season (Miller and Ozoga 1997). A study on movements of male white-tailed deer in Oklahoma found that juveniles (1.5 - 2.5 years-old) exerted the most effort during the pre-rut, with generally greater mean movement rates and path tortuosity during the pre-rut than older males (Holtfreter 2008). In contrast, older males exerted the greatest effort during the rut and post-rut, which was when juveniles decreased their path tortuosity. Juveniles may focus their breeding efforts on does that come into estrous early, thus avoiding competing with older, more experienced males that wait until the rut to expend effort. In essence, juvenile reproductive effort was suppressed by older males during the rut. Suppression of breeding effort in young males has also been documented in red deer (Pemberton et al. 1992). During the rut, young red deer males experienced minimal weight loss compared to prime-aged males because they did not rut as long or relied on the “sneaker” method that is less energetically costly than harem-holding (Yoccoz et al. 2002). This study also hypothesized that prime-aged males put the most effort into the rut because they would be the most successful while younger males put in less effort because they would most likely be less successful. Moreover, Ditchkoff (2001b) found that younger males had reduced risk of natural mortality while mature males had roughly equal probabilities of natural mortality and human-induced mortality in populations with a significant proportion of mature males. Ditchkoff et al. (2001b) hypothesized that younger males were exerting less effort in reproduction due to their reduced probability of success.

Although older males are more reproductively successful than young males, they do not completely exclude young males from breeding opportunities and reproductive success. In white-tailed deer, though individual dominant males may be very successful for one year, there is a high degree of variability in breeding success. This variability suggests that males who are most successful are constantly changing and that individual males may be unable to dominate breeding through consecutive years (Mathews and Porter 1993). In a penned study, though prime-aged males were dominant, dominance ranks were not stable throughout the duration of the study and males >3 years old had only a weak association between age and dominance (DeYoung et al. 2006). Changes in dominance may have been reflected in the presence of multiple paternities in about 25% of compound litters. Additionally, multiple paternities occurred when there were multiple does in estrous at once, indicating that a single dominant prime-aged male couldn't monopolize multiple estrous females in captivity (DeYoung et al. 2009b). DeYoung et al. (2009a) also studied several free-ranging populations and found that despite varying population demographics, many males breed including significant contributions from young males. As mentioned before, the study by Sorin (2004) on a simulated free-ranging population reinforced DeYoung et al.'s (2009a) results because multiple paternities were found in 22% of compound litters and all male age classes other than fawns were reproductively successful. Young fallow deer also successfully turn to alternate mating strategies (e.g., entering territories belonging to other males or chasing females away from territory holders) to gain reproductive success they would not otherwise gain (Komers et al. 1997). In bighorn rams (*Ovis canadensis*), younger males are able to sire roughly the same proportion of offspring as older males by relying on the alternate mating strategy of coursing. This strategy results in many individuals siring a few offspring each, as opposed to older males that use a tending strategy that results in a few individuals each siring many offspring (Coltman et al. 2002).

Older males may be more successful than younger males as an age class for a number of reasons. In a study examining relative fluctuating asymmetry in antlers as an indicator of quality, Ditchkoff et al. (2001a) found that relative fluctuating asymmetry decreased as buck age increased. The reason for the decrease in asymmetry was hypothesized to be due to the removal of less-fit individuals with time, leaving a population that is of better quality and greater relative symmetry. If true, the hypothesis would suggest that older buck age classes would consist of more skilled and desirable competitors than the yearling age class. However, the study also found that after 6.5 years of age, buck antler size and relative fluctuating asymmetry exhibited no relationship, indicating that 6.5 year olds may reach the nutritional threshold for antler growth at which point antler size no longer increases with age. The lack of a relationship could also indicate that some older males increase their antler size and sacrifice nutrients, putting themselves in greater nutritional stress during the rut as a last-ditch effort to breed which would cause their relative fluctuating asymmetry to increase. It is possible that at 6.5 years of age, white-tailed deer males may begin to enter senescence and be less competitive breeders, creating an age-range where bucks are best able to compete for mates.

Body Size

Body size is a factor commonly associated with male reproductive success. Typically, males with larger bodies are more victorious in intrasexual conflicts for mates and therefore more reproductively successful. A penned study on white-tailed deer found that the heaviest males were always initially dominant and were the most successful in siring fawns (DeYoung et al. 2006). Dominant (e.g., heavy) males sired 4 - 17 offspring each as compared to the 0 - 1 that most subordinate males were able to sire. In total, 87.6% of fawns were sired by dominant males. In one pen where a 2.5 year-old male was heaviest and dominant, one of the two yearlings in the pen was able to sire 7 fawns, more offspring than any of the other subordinate deer, perhaps because he was 16.2 kg heavier on average than the other 6 yearlings and nearly as heavy as the dominant 2.5 year-old male in his pen. Male red deer on the Isle of Rhum also exhibit a connection between body size and reproductive success via fighting success (Clutton-Brock et al. 1979). Body size in male red deer peaks at 6 years of age and declines after 11. Because body size is a major factor in fighting success and fighting success is closely related to reproductive success, both fighting success and reproductive success peak at 7 - 10 years. Northern elephant seals (*Mirounga angustirostris*) also demonstrate a positive correlation between size and dominance rank, as well as a positive correlation between dominance rank and copulatory success (Haley et al. 1994).

In most species, male body size contributes to reproductive success via the relationship between body size and dominance rank. Larger males are more victorious in male-male conflicts and therefore attain greater dominance. Greater dominance in turn increases reproductive success via access to more females, longer access to females, or access to a location where more females are located, etc. DeYoung et al.'s (2006) study on penned white-tailed deer found that the heaviest male in each pen was initially dominant. In two of the six pens, dominance was not permanent and a male that was initially subordinate became dominant. Because male body weight no longer increases steadily with age after 3.5 years and males ≥3.5 years of age tend to have similar weights, the heaviest male may not always be dominant, and lighter males may be dominant over heavy males. Another study using penned white-tailed deer found that weight and age accounted for 70% of male rank variation (Townsend and Bailey 1981). However, male rank changed with weight regardless of age because weight is related to strength and endurance in fighting. Strength and endurance seemed to be the deciding factors in determining which males won fights. The model created by the researchers to explain male dominance rank explained about 70% of the observed variation and weight accounted for the majority of the model's variation. A similar pattern was found in male red deer (Clutton-Brock et al. 1979). Increased body size leads to increased fighting success due to greater strength and endurance and dominant males are able to claim and maintain territories where greater numbers of hinds congregate during the rut, increasing their reproductive success. Successful fighters are also able to repel attempts by rival males seeking to separate and steal hinds from harems. Body size also serves as a determinant of which red deer males may fight each other for dominance as males tend to fight only similarly-sized males because smaller males will back down from a fight before it occurs. Because of this, dominance ranks and reproductive success were the most variable among mature males (6 years and older) when body size peaks and age is no longer a determinant of size. Northern elephant seals also show a correlation between body size, dominance, and copulatory success (Haley et al. 1994). Arrival size, the size of male elephant seals when they first arrive at breeding grounds in particular is linked with male elephant seal dominance rank because high-ranking males can lose a greater proportion of their body weight (≤46%) than low-ranking males during the breeding season. Large male elephant seals are more victorious in fights and are therefore able to secure the most mating opportunities as dominant males with size variation accounting for 16 - 44% of dominance variation.

Besides providing an advantage in intrasexual conflicts, large body size may also provide an honest signal of the genotypic quality of a male. Ditchkoff et al. (2001c) found that heterozygosity at MHC loci was associated positively with large male body size which may be due to a lifetime advantage from a stronger immune system. Additionally, MHC-heterozygous males had greater serum testosterone concentrations than males that were homozygous at the MHC. Testosterone drives reproductive behavior in male white-tailed deer (Miller et al. 1987) and males with greater concentrations should be the most aggressive in intrasexual conflicts and show an increase in displays which may increase their dominance rank and reproductive success. Overall, males with large bodies may be honestly advertising their greater quality and thus may be able to gain dominance and reproductive success.

Though heavier males tend to be more dominant and more reproductively successful they are unable to completely exclude lighter males from breeding opportunities. As discussed previously, dominance was not constant throughout DeYoung et al.'s (2006) penned study and in both cases where dominance shifted, a lighter male supplanted the heaviest male as dominant. Additionally, the heaviest yearling was able to sire 7 fawns to the 14 sired by the dominant 2.5 year-old and the 1 sired by the other subordinate yearling. The successful yearling shared paternity of 3 litters with the 2.5 year-old male and independently sired 2 litters. In total, multiple paternities were detected in about 25% of compound litters. Multiple paternities occurred when multiple does were in estrous at once, indicating that a single large dominant male couldn't monopolize multiple estrous females in captivity. DeYoung et al. (2009a) also studied several free-ranging populations and found that despite varying population demographics, many males breed including significant contributions from young (e.g., light) males. A study by Sorin (2004) on a free-ranging population of white-tailed deer reinforced DeYoung et al.'s (2009b) results because multiple paternities were found in 22% of compound litters and all male age classes other than fawns were reproductively successful. In red deer, young males adopt a "sneaker" method which allows them to sire a few calves that they would not have otherwise been able to sire (Pemberton et al. 1992, Yoccoz et al. 2002).

Ornamentation

Ornaments are secondary sexual characteristics that serve to enhance reproductive opportunity either by attracting members of the opposite sex or by aiding in intrasexual conflicts for mating opportunities. For example, brightly colored patches of feathers on birds (blue grosbeaks, *Passerina caerulea*, Keyser and Hill 2000; eastern blue birds, *Sialia sialis*, Siefferman and Hill 2003), skin growths and spurs on birds (wild turkeys, *Meleagris gallopavo*, Buchholz 1995; pheasants, *Phasianus colchicus*, von Schantz et al. 1996), and antlers or horns on ungulates (white-tailed deer, Ditchkoff et al. 2001a; Soay sheep, *Ovis aries*, Preston et al. 2003; roe deer, *Capreolus capreolus*, Vanpe et al. 2007) are all ornaments. In white-tailed deer, males are ornamented with antlers that grow and are shed seasonally. If conditions are good, antlers will typically increase in size and/or complexity (i.e. number of points) every year until senescence (Ditchkoff et al. 2001a). During the breeding season, bucks use their antlers in intrasexual combat to establish dominance and compete for the chance to mate with receptive does.

Reproductive success tends to be associated positively with degree of ornamentation such that males with more extreme ornaments are more reproductively successful. There are two hypotheses that seek to explain this phenomenon and the first states that females arbitrarily prefer more ornamented individuals and thus increase the frequency and degree of ornamentation through selective mating (Fisher and Bennett 1999). The second hypothesis, also known as the good genes hypothesis, states that ornamentation is an honest indicator of fitness used by members of the opposite sex to judge desirability as a mate (Hamilton and Zuk 1982, Zahavi et al. 1999). Ornamentation may signify fitness by indicating a less obvious trait that has strong effects on survival (Hamilton and Zuk 1982) and by demonstrating the ability of a male to survive despite expending energy on a character that does not directly impact and may even hinder survival (Zahavi et al. 1999). Costly ornaments ensure that only males who are genuinely high quality individuals can afford to produce the ornaments, thus ensuring that ornaments are honest signals (Zahavi et al. 1999). Peacock tails, for example, are energetically costly to produce and maintain (Walther and Clayton 2005) but accurately signal the immune system strength of the males to potential mates (Moller and Petrie 2002, Loyau et al. 2005). Similarly, Bucholz (1995) found that portions of male wild turkey ornaments were associated with specific immune responses. For example, the degree of ornamentation of the frontal caruncle area was associated negatively with the summed burden of blood parasites while relaxed snood length was associated negatively with counts of fecal coccidian oocysts. Male pheasants are ornamented with heel spurs that are used during intrasexual combat for mates and are associated with male age, weight, size, and access to food as a juvenile (von Schantz et al. 1989). In addition to providing an advantage during combat, long spurs are significantly affected by MHC genotype, such that male pheasants that are MHC heterozygotes have longer spurs and greater survival than MHC homozygotes (von Schantz et al. 1996). Male blue grosbeaks use color as ornamentation where degree of blueness is associated positively with male body size, territory size, and prey availability (Keyser and Hill 2000). In addition, Keyser and Hill (2000) found that blueness may also be associated positively with male parental care. Siefferman and Hill (2003) studied a population of eastern bluebirds and found that plumage color was associated positively with male parental care, offspring condition, male reproductive success, and first egg date.

Antlers are also honest signals of male quality since they are arguably the fastest growing tissue in the animal kingdom and thus are extremely costly to grow. In addition to demonstrating that a male can expend the resources to generate large antlers, antler size is also indicative of male quality. For example, Malo et al. (2005) found that relative antler size and complexity were associated positively with testes size, sperm production, and sperm velocity in red deer, with no significant influence from kidney fat or population size. Specifically, relative testes size accounted for 15.37% of the explained relative antler size variance and sperm velocity accounted for 8.12%. Red deer males with large antlers are more competitive for reproductive opportunities both because of their advantage in fights and because of their advantage in sperm competition. Vanpe et al. (2007) studied three populations of roe deer in Europe and found in all three populations that antler size increased with body mass and age until senescence, independent of environmental conditions. Roe deer antlers are honest signals of male quality because they were not influenced by environmental conditions but were influenced by the quality of the individual (i.e., body mass and age). Pelabon and van Breukelen (1998) also assessed the reliability of roe deer antlers as signals of quality by examining antler asymmetry with regards to age, population density, and condition. If antlers honestly signal male quality, then individuals who are young or in poor condition will have asymmetrical antlers due to allocating resources toward functions other than antler growth. Results of Pelabon and van Breukelen (1998) support the concept that roe deer antlers are honest signals because antler asymmetry decreased with age but increased as body mass and population density increased. Males that were of prime age, had greater body mass, and lived in a population with lower density had the most symmetrical antlers, potentially signaling their superior quality.

Bowyer et al. (2001) performed a similar study with moose (*Alces alces*) and found that fluctuating asymmetry of palm characteristics was associated negatively with antler size. Moose antlers, therefore, may potentially be honest signals of male quality because only high quality males (i.e., high fitness males) can afford the nutritional demands necessary to produce large antlers. Reindeer (*Rangifer tarandus*) antlers also exhibit fluctuation asymmetry associated negatively with antler size (Markusson and Folstad 1997). Additionally, the study found that reindeer antler length, weight, and volume were all associated positively with body weight, and asymmetry in antler length, volume, and weight were associated positively with parasite index. Consequently, asymmetry in reindeer antlers could indicate which males are in poor condition and have weaker immune systems. Ditchkoff et al. (2001a) found evidence of fluctuating asymmetry in white-tailed deer antlers and reported that antler size and age were both associated negatively with relative fluctuating asymmetry. Moreover, Ditchkoff et al. (2001a) noted that that MHC heterozygosity in male white-tailed deer was associated positively with several antler characteristics, including Boone and Crockett antler score, basal circumference, and number of points. Antler characteristics were also associated positively with age and serum testosterone levels but associated negatively with total abundance of abomasal nematodes. Males that had large, well-developed antlers tended to have stronger immune systems as demonstrated by MHC haplotype and abomasal nematode abundance despite greater serum testosterone levels. As a result, it is likely that white-tailed deer antlers were honest signals of male quality.

More extreme ornamentation has been shown to be associated with reproductive success in a number of species. For example, more elaborate peacock (*Pavo cristatus*) tails with a greater number of eyespots were associated with increased reproductive success (Petrie et al. 1991) as was tail length (Petrie and Halliday 1994). Petrie and Williams (1993) also found that peahens invested more into reproduction by producing more eggs when mated to more ornamented males. Male ornamentation has also been linked to reproductive success in eastern bluebirds, in that more ornamented males (i.e., males with more ultraviolet and pure-blue UV-colored plumage) had greater reproductive success (Siefferman and Hill 2003). Göransson et al. (1990) found that male spur length in pheasants was the greatest predictor of harem size and associated with phenotypic conditions and viability, even when age and body size were controlled for. Overall, spur length in male pheasants was found to predict male reproductive success most accurately. In turkeys, male ornamentation has also been found to be associated with reproductive success (Buchholz 1995). Specifically, female turkeys solicited copulations primarily from males with longer snoods and wider skull caps, and spent more time close to the more ornamented male. Female turkeys behaved the same way when presented with an unmanipulated decoy male and a manipulated decoy that had a longer snood and more side caruncles.

Increased reproductive success in highly ornamented males has also been documented in mammalian species. For example, Preston et al. (2003) found that horn length in male Soay sheep was associated with access to receptive females, successful defense of estrous females, and paternity success. In red deer, antler mass was found to have a significant effect on annual breeding success and lifetime average antler mass was found to have a significant effect on total lifetime breeding success (Kruuk et al. 2002). The authors speculated that greater antler mass enabled a male to be a stronger competitor in intrasexual combat, thus acquiring and defending larger harems, and increasing reproductive success. However, Malo et al. (2005) argued that large-antlered males were more successful because relative antler size indicates sperm production and velocity, as they found that relative testes size and sperm velocity explained significant portions of variance in relative antler size (15.37% and 8.12%, respectively). Increased sperm production and velocity may allow males to increase fertilization and make them more competitive in case of sperm competition. Relatively little work has been done on the effect of ornamentation on reproductive success in members of the genus *Odocoileus*. Bowyer (1986) observed that large antler size in male southern mule deer (*Odocoileus hemionus fuliginatus*) was associated with dominance. Additionally, both of the two copulations observed involved large-antlered bucks. White-tailed deer are expected to share the same relationship between ornamentation and dominance. Dominance increases reproductive success in white-tailed deer (DeYoung et al. 2006), likely through winning intrasexual conflicts for breeding opportunities similar to the patterns shown in red deer (Clutton-Brock et al. 1979) and fallow deer (Komers et al. 1997).

Mate Selection

Mate choice is an important factor in maximizing an individual's fitness as high quality mates help to increase reproductive success, offspring survival, and offspring reproductive success. Female mate choice has been observed in a number of species with varying mating strategies. Lekking species clearly exhibit female mate choice as the males will gather and display to females who visit and inspect several males before initiating copulation with a single male. For example, spotted bowerbird (*Chlamydera maculata*) males build bowers and decorate them with objects that can include vegetation, fruit, glass, and bones (Borgia 1995). Females visit and inspect several male bowers and are recipients of mating displays at each, before choosing a male to visit and initiate copulation with. Fallow deer are an ungulate species that form leks and females will approach and inspect several males before selecting one to copulate with (Apollonio et al. 1989). In fallow deer, females can also increase their options in mates by delaying the onset of ovulation when they encounter only socially immature males but are exposed to mating stimuli from socially mature males (Komers et al. 1999).

Socially monogamous species also have been observed to exhibit female choice. For example, house finch (*Carpodacus mexicanus*) males have patches of pigmented feathers that can range from yellow to red depending on diet quality and carotenoid composition (Hill 1990). Females prefer more colorful and brighter males (i.e., redder; Hill 1990) resulting in brighter males being more likely to pair and pair earlier (Hill 1994, Hill et al. 1999). Additionally, female preference for bright house finch males was consistent in widespread populations including Hawaii, Michigan, and California (Hill 1994) as well as remaining temporally consistent over a six year study of populations in Michigan and Alabama (Hill et al. 1999).

Evidence of female choice has also been found in species with harem-based mating systems. Male pheasants establish territories that females visit before they choose to settle in a single territory with other females that have made the same choice (von Schantz et al. 1989). Females may choose to move to a different male's harem but will copulate with the male whose territory they have settled in when they are receptive. Red deer also utilize a harem system where males attempt to herd females into a harem group, though females may leave and join a different harem (Clutton-Brock et al. 1982). Charlton et al. (2007) found that estrus females took more steps toward a speaker playing roars from a simulated large stag than toward a speaker playing roars from a simulated small stag.

Female choice has also been observed in species practicing a scramble mating system, the mating system utilized by white-tailed deer. A great deal of research has been done on female choice in guppies (*Poecilia reticulata*), a species where male tail size and coloration varies greatly. Male guppies search for females and proceed to display upon finding them (Bischoff et al. 1985, Houde and Endler 1990). Females may then choose to allow the male to copulate or to ignore him and copulate with another more desirable male that has a larger tail, faster display rate (Bischoff et al. 1985), or a greater proportion of orange on the body and tail (Houde and Endler 1990).

When choosing mates, females make selections based on a standard set of criteria that varies between species but can also vary by populations within a species. Houde and Endler (1990) found that female guppies from populations where male tails on average have little orange pigmentation had little or no preference for the area of orange on a male's tail. On the other hand, female guppies from populations where males have a substantial amount of orange pigmentation had a strong preference for greater area of orange on a male's tail.

The traits that females use to choose mates can either be based on arbitrary preference or on traits signaling that the male can confer benefits for the female and/or her offspring. However, many traits subject to female choice have been discovered to be honest signals of male quality. In the socially monogamous house finch, male ornamentation in the form of plumage pigmentation was found to be associated with the rate at which males fed their mates and chicks such that brighter males exhibited greater feed rates and were less likely to be abandoned by their mates (Hill 1991). Male house finch pigmentation was also associated with survival (Hill 1990) and foraging ability since the pigmentation is based on dietary carotenoid (Hill 1991). Also, the male offspring of brighter males were more likely to be brightly colored themselves, potentially signaling a genetic advantage conferred by females selecting high quality mates (Hill 1991).

Female pheasants preferred males with longer spurs which are associated with male MHC haplotype (von Schantz et al. 1996) and age, body size, weight, and survival (Göransson et al. 1990). Additionally, von Schantz et al. (1989) found that 13% of female reproductive success was predicted by male spur length. Therefore, female pheasants tend to select mates that are in good condition, MHC heterozygous, and can increase the female's reproductive success. Turkey females select males based on the extent of head and neck ornamentation (Buchholz 1995). Males with longer snoods and wider skull caps were more likely to be approached and have copulations solicited by females than same-aged males with shorter snoods and narrower skull caps. Snood length and skull cap size were found to be associated negatively with parasite loads, providing an honest signal that the females could use to determine which males were healthiest and potentially had the strongest immune systems.

Apollonio et al. (1989) found that female fallow deer tended to select males that occupied high quality territories in the lek resulting in the dominant males obtaining most of the copulations. In addition, Clutton-Brock et al. (1989) found that experimentally-induced territory change did not affect which males were most reproductively successful, indicating that female fallow deer base their choice on phenotypic quality rather than territory quality. Though little support was found for female choice in a red deer population on the Isle of Rhum (Clutton-Brock et al. 1982), McComb (1991) found that captive female red deer preferred males that were roaring bout leaders, as signaled by females approaching speakers that played roars as the bout leader. Bout leaders would likely be males that are in good condition and able to expend the energy to roar more rapidly and more often. Moreover, Charlton et al. (2007) found that estrous females took more steps toward speakers that played roars that simulated larger males than speakers that played roars that simulated small males. In red deer, females were able to select higher quality mates by sound displays alone because larger males have greater fighting success and are more dominant (Clutton-Brock et al. 1979), and males are unable to falsely advertise their size by sound due to the inherent relationship between sound and vocal tract size (Charlton et al. 2007).

Although mating systems and preferred traits may vary across species, female choice is generally exhibited by females approaching the selected male and soliciting copulation. For example, female guppies respond to male mating displays by approaching and remaining near the male guppy and by giving a sexual display response to solicit copulation (Bischoff et al. 1985, Houde and Endler 1990). House finch females will approach the selected male and posture to initiate pair bonding behaviors (Hill 1990). Female spotted bowerbirds will approach the selected male and enter the bower, where they posture to initiate copulation (Borgia and Mueller 1992, Borgia 1995). In pheasants, females visit multiple males before they set up their home range within the territory of their selected male and they will copulate with him when they are receptive (von Schantz et al. 1989). Similarly, in lekking fallow deer, females will inspect several males before selecting one to copulate with (Apollonio et al. 1989). Red deer does displayed female choice in experiments where they judged male quality by nuances in roars and showed selection by consistently moving toward one speaker (McComb 1991, Charlton et al. 2007). Female red deer in a wild population could also display choice by selecting which male's harem to join and by initiating copulation with a male of interest by approaching him while in estrus (Clutton-Brock et al. 1982).

While it is likely that female white-tailed deer exhibit mate choice at some level, little has been done to study the phenomenon. There is the potential for does to evaluate males on several traits including phenotypic characteristics and chemical markers. Ditchkoff et al. (2001a) found that relative asymmetry of white-tailed deer antlers was associated negatively with body mass, body length, and antler development. In addition, white-tailed deer antler scores and development were found to correlate with MHC heterzygosity (Ditchkoff et al. 2001c). Males with symmetrical, well-developed antlers are more likely to be large, MHC heterozygotes, and able to produce energetically costly ornaments and maintain immune function despite experiencing testosterone-induced immune suppression. Buck body size also serves as an honest signal of male quality as DeYoung et al. (2006) concluded that larger males were more dominant in the male hierarchy, and Ditchkoff et al. (2001c) found that MHC heterozygous males tended to be larger.

Male white-tailed deer also engage in extensive scent marking during the breeding season where they create rubs on tree trunks and scrapes on the ground. Rubs are formed by bucks repeatedly rubbing their forehead and antlers on a tree trunk, a process that both removes the tree bark and leaves chemical compounds produced in scent glands on the tree trunk. Atkeson and Marchinton (1982) found that activity of buck forehead glands peaks during the rut and are greatest in dominant males. Additionally, Gassett et al. (1997) analyzed the secretions from buck forehead glands and identified 57 different compounds, one of which was more concentrated on the forehead hair of dominant males and eight of which were more concentrated on the hair of subordinate males. Because of potential differences in the chemical composition forehead secretions between dominant and subordinate bucks, does may be able to determine the quality of the males frequenting that rub. Bucks also create scrapes during the rut which are areas where the leaves are scraped away leaving patches of bare ground typically found under or near a rub where bucks may rub-urinate. Rub-urination involves the buck urinating on the tarsal glands and both urine and tarsal gland secretions leave a chemical signpost that the buck has been there. Miller et al. (1998) examined urine samples from white-tailed deer bucks and isolated 55 different chemical compounds. Of special interest was that during the breeding season three chemicals were more abundant in urine from dominant males, nine were found solely in urine from dominant males, and nineteen were found only in urine from subordinate males. White-tailed deer also have interdigital scent glands that produce chemical signals to communicate male social rank (Gassett et al. 1996). Specifically, 11 of 46 compounds were more concentrated in secretions from dominant bucks. Though there is little evidence regarding doe use of buck scent marks, Alexy et al. (2001) found that whereas bucks were more likely to interact with scrapes, does were much more likely to visit the scrapes. Therefore, chemical compounds left behind by bucks at rubs and scrapes may be used by does to determine the social status of bucks frequenting those sites.

In addition to the existence of potential traits that does could use to discriminate between potential mates, Ozoga and Verme (1985) observed that yearling does in a 252 ha enclosure tended to be bred earlier than mature does and were more likely to be bred by yearling bucks, a buck age group that had very low reproductive success. Moreover, they observed that yearling does sometimes acted intimidated by mature bucks and fled without copulating whereas mature does tended to act aggressively toward yearling bucks regardless of whether the buck was attempting to court the doe. Due to these observations, Ozoga and Verme (1985) hypothesized that does may be more receptive when they are courted by similar-aged bucks. Therefore, there are both physical and chemical traits in white-tailed deer that have the potential to be employed by does to discriminate between potential mates. Though very little evidence is available as to the extent that does exercise female choice, it is likely that it occurs to some degree because does have the ability to avoid and repel unwanted suitors.

Inbreeding Avoidance

Leading Theories

Inbreeding is a topic of concern for many species, particularly those that have a limited genetic pool to draw from such as endangered species or species that are unable to travel and disperse as they did historically before fences, roads, and human development fragmented potential habitat and travel corridors. For such species, inbreeding can begin to have a negative effect on the fitness of inbred individuals (e.g., inbreeding depression) typically resulting in increased mortality of young and adults and reduced reproductive capability in surviving adults. For example, Jimènez et al. (1994) released inbred and non-inbred white-footed mice (*Peromyscus leucopus noveboracensis*) into a field site and retrapped them to examine body weight and survival. They found that inbred mice had lesser survival compared to non-inbred mice; weekly survival that was only 56% of the non-inbred mice. Additionally, whereas female mice showed no effect of inbreeding on body weight after release, inbred male mice lost weight throughout the recapture period while non-inbred males maintained their weight. In a study with *Arianta arbustorum* snails, Chen (1993) crossed sibling pairs and unrelated pairs and compared number of eggs laid, proportion of eggs that hatched, and hatchling survival. Though there was no difference in the number of eggs laid, inbred pairs had fewer eggs hatch than unrelated pairs (30.4% vs. 48.5%) and reduced survival of hatchlings in the wild (Chen 1993). Finally, Slate et al. (2000) found that inbreeding depression in red deer resulted in lower lifetime breeding success in both males and females. With genetic techniques becoming more common, further study of inbreeding and inbreeding avoidance mechanisms in wild free-ranging populations is warranted.

Pusey and Wolf (1996) present four mechanisms by which species avoid inbreeding: dispersal, extra-pair or extra-group copulations, recognition and avoidance of kin as mates, and delayed maturation or reproductive suppression. Fadao et al. (2002) also list dispersal and avoidance of kin as two common inbreeding avoidance mechanisms. Inbreeding avoidance by dispersal occurs when individuals leave their natal home range in order to avoid breeding with relatives who remain in the natal home range. For example, Lambin (1994) found evidence of inbreeding avoidance due to dispersal in male Townsend's voles (*Microtus townsendii*). Female voles tended to establish home ranges very close to their natal home range but male voles tended to disperse much farther and in a different direction than dispersing sisters (Lambin 1994). Male vole dispersal was strongly influenced by the presence of the mother or full sisters in the maternal home range during maturation. The factors involved in triggering dispersal are under debate, as intrasexual competition and resource competition have both been proposed as alternate causes of dispersal. Pusey and Wolf (1996) suggest that dispersal may be caused by the interplay of inbreeding avoidance, intrasexual competition, and resource competition. Lehmann and Perron (2003) suggest that male dispersal may be caused by females suppressing estrus when near related males and by soliciting copulations with unrelated males.

Extra-pair and extra-group copulations tend to occur in monogamous species where a female paired with a related male will copulate with an unrelated male while remaining bonded with her partner. For example, Sillero-Zubiri et al. (1996) studied behaviorally monogamous Ethiopian wolves (*Canis simensis*) in a saturated habitat that discouraged dispersal as an inbreeding avoidance mechanism (76% of offspring did not disperse during the study). Because offspring tended to remain in their natal group and move up the social hierarchy there was potential for inbreeding to occur as there were several cases of parent-offspring pairing and sibling pairing. Despite the potential for inbreeding, 70% of observed copulations occurred between females and non-pack males. Additionally, females would only mate with the alpha male of their own pack but did not discriminate strongly by status among males from other packs. It appears that extra-pack copulations are a significant method of inbreeding avoidance in Ethiopian wolves when dispersal is not a viable option.

The third inbreeding avoidance mechanism is kin recognition and avoidance as mates which occurs when individuals recognize a potential mate as a relative and avoid copulating with them. One example of kin recognition and avoidance as inbreeding avoidance occurs in the African elephant (*Loxodonta africana*) where males avoid engaging in reproductive behaviors with closely related individuals including maternal and paternal kin (Archie et al. 2007). Because elephants are polygynous with females traveling in matriarchal groups and males traveling alone, an individual may not associate closely with its paternal relatives as a juvenile. Regardless of acquaintance, male elephants are able to distinguish close genetic relatives and avoid them as mates resulting in only 3.29% of parental pairs being close relatives.

Inbreeding can also be avoided by delayed maturation or reproductive suppression while in the presence of closely related individuals such as a parent. Female pine vole (*Microtus pinetorum*) maturation, for example, is delayed by the presence of chemical signals contained in parental urine (Lepri and Vandenbergh 1986). Uterine and ovarian weight, a measure of sexual maturity, was significantly less in females exposed to stud males and parental urine when compared to females exposed to only stud males. Parental inhibition of offspring reproduction can reduce inbreeding by decreasing the likelihood that offspring will mate with each other or a parent as long as they remain in the family unit.

Male white-tailed deer yearlings traditionally disperse from the maternal home range while yearling does set up a home range adjacent to, and sometimes overlapping, the maternal home range. Reported dispersal rates of yearling bucks vary widely, likely due in part to varying habitat types and population demographics. Woodson et al. (1980) studied a population in Virginia and reported an estimated 13% of male fawns dispersed while Hawkins and Klimstra (1970) studied a population in Illinois and reported that 80% of yearling bucks emigrated. Numerous other studies found dispersal rates intermediate to those of Woodson et al. (1980) and Klimstra (1970) (50%, Kammermeyer and Marchinton (1976); 51%, Nixon et al. (1991); 35%, Hölzenbein and Marchinton (1992);

64%, Nelson (1993); 70%, Rosenberry et al. (1999); 74% Long et al. (2005). Dispersal distance also varies across studies; male fawns in Illinois dispersed an average of 40.9 ± 5.0 km (Nixon et al. 1991) while yearling bucks in Pennsylvania dispersed an average of 8.0±0.61 km on the Allegheny Plateau and 7.0 ± 1.0 km in the Ridge and Valley region of Centre County (Long et al. 2005). Holzenbein and Marchinton (1992) found that dispersing male fawns either dispersed gradually over a relatively short distance that averaged 1.1 km, or abruptly over a relatively long distance that averaged 4.1 km.

Local mate competition and antagonism by related females (inbreeding avoidance) are the two mechanisms of dispersal that are commonly accepted. Because fawns and yearlings are poor breeding competitors, local mate competition reasons that they would disperse to a new area with fewer competitors for mates. On the other hand, does that are aggressive toward young related bucks could push these individuals out of the maternal home range to avoid inbreeding, thus raising the fitness of both the does and the bucks. Rosenberry et al. (2001) found that dispersing yearlings were more subordinate than non-dispersers and were the only yearlings that engaged in breeding behavior with adult bucks. Additionally, they did not observe any aggressive behaviors by adult females making it likely that in the study population, sexual competition played a large role in motivating yearling buck dispersal. However, in a population with very few mature males, Ozoga and Verme (1985) observed that yearling bucks still dispersed and hypothesized that related does may have caused the bucks to disperse, indicating a possible inbreeding avoidance mechanism. They also observed that adult does in the study population were dominant over related yearling bucks and avoided them but were usually submissive to unrelated yearling bucks.

In most populations, yearling buck dispersal is likely influenced by a combination of sexual competition and inbreeding avoidance. Orphaned male fawns, therefore, might be expected to show reduced rates of dispersal because they lack the antagonistic interactions with related females to push them into new home ranges. Holzenbein and Marchinton (1992) tracked 13 orphaned male fawns and 10 non-orphaned male fawns until they were all at least 2.5 years of age and found that 7 of the 10 non-orphans dispersed while only 1 of the orphans dispersed. Food competition was not considered a factor for dispersal because dispersal occurred during the spring and fall when food was abundant. However, Woodson et al. (1980) found that 5 of 21 orphans dispersed while only 2 of 31 non-orphans dispersed. Additionally, Nixon et al. (1991) observed that 67% of their marked male orphans dispersed versus 57% of their marked non-orphans, and Rosenberry et al. (2001) did not observe any antagonistic interactions between adult females and yearlings that would explain yearling dispersal. It may be that in certain populations, conditions may limit the effect of inbreeding avoidance as a mechanism of yearling buck dispersal leading to philopatric orphans.

It is possible that white-tailed deer utilize inbreeding avoidance mechanisms, including dispersal. However, captive deer (e.g., populations enclosed in high-fenced properties) may be limited in their ability to disperse. Additionally, the lack of pair-bonds or long-term associations between males and females in white-tailed deer means that extra-pair/extra-group copulations and delayed maturation/reproductive suppression are unlikely to be significant mechanisms of inbreeding avoidance in captive white-tailed deer populations. Because dispersal may be limited, recognition and avoidance of kin are likely the primary mechanisms at work in captive populations.

Mechanisms of Kin Recognition

To some extent, all of the inbreeding avoidance mechanisms require an animal to identify related individuals and differentiate them from unrelated individuals. Kin recognition is widely accepted as a function of two mechanisms, recognition by association and phenotype matching (Fadao et al. 2002). Recognition by association, or familiarity, occurs when an animal recognizes those it encountered at a young age as kin. Phenotype matching occurs when an animal compares others to a phenotypic standard, typically that of their parents or themselves.

When discussing kin recognition by familiarity, it is generally accepted that the pre-weaning period is when an individual learns to recognize those it associates closely with as kin. During this time period, it is unlikely that the young would be exposed to other individuals that are not closely related to them, minimizing the risk that unrelated individuals would be recognized as kin (Fadao et al. 2002). Kin recognition by familiarity can be examined in a laboratory setting by pairing siblings raised apart, siblings raised together, non-siblings raised apart, and non-siblings raised together. Researchers then compare several reproductive characteristics such as what proportion of pairs in each category produced litters, number of pups per litter, number of days from pairing to birth of first litter, etc. Fadao et al. (2002) examined kin recognition in mandarin voles (*Microtus mandarinus*) and found that non-siblings raised apart produced the most litters, with 81% of non-sibling pairs raised apart producing litters as compared to 8% of siblings raised together, 10% of non-siblings raised together, and 30% of siblings raised apart. In general, individuals raised apart produced significantly more litters than individuals reared together, clearly demonstrating that kin recognition by familiarity is at play in mandarin voles. The striped mouse (*Rhabdomys pumilio*) also exhibits kin recognition by familiarity as daughters housed with their fathers had less developed uteri and were less likely to produce litters than females housed with unfamiliar males (15.3 mg vs. 28.2 mg and 20% pregnancy rate vs. 73.3% pregnancy rate, respectively; Pillay 2002). Additionally, females housed with their foster fathers had less developed uteri and were less likely to produce litters than females that were fostered at birth and then reintroduced to their biological fathers as adults (15.1 mg vs. 27.7 mg and 6.7% pregnancy rate vs. 60% pregnancy rate, respectively). Exposure to a male during the pre-weaning period caused females to recognize that male as family and thus avoid him as a mate.

Unlike kin recognition by familiarity, phenotype matching is not dependent on a period of association. The study on mandarin voles by Fadao et al. (2002) also found that sibling pairs produced statistically similar numbers of litters regardless of whether they were raised together or apart. Furthermore, siblings raised apart produced significantly fewer litters than non-siblings raised apart. Phenotype matching accounts for the ability of siblings to recognize each other as relatives despite having been separated at birth which eliminates kin recognition by familiarity as the reason siblings produced fewer litters together. Also, there was no significant difference in the percentage of sibling-pairs that produced litters, when the pairs were separated at different pre-weaning ages. The lack of effect could be due to phenotype matching where siblings used phenotype matching and had no association period required to recognize each other as relatives, thus avoiding each other as mates. Fadao et al. (2002) found that mandarin voles do not "forget" their kin when reared apart regardless of whether they were separated at birth or at some later time. Archie et al. (2007) found that male African elephants could identify and avoid mating with closely related kin even those that were paternally related and had not been in close contact with the males. Social rules would be excessively cumbersome for males to accurately exclude closely related kin and would likely result in males avoiding a number of unrelated females along with the related females. This suggested that phenotype matching is the possible mechanism of kin recognition in African elephants.

An increasing number of studies on phenotype matching are focusing on the role of the MHC in kin recognition. Heterozygosity at MHC loci provides an individual with a greater range of immune protection than homozygosity by allowing the body to recognize a greater range of antigens as threats. The MHC has been documented as affecting mate selection in a number of species, including humans (Wedekind et al. 1995, Ober et al. 1997), ring-necked pheasants (von Schantz et al. 1996), and mice (Beauchamp et al. 1988, Eklund 1997), and it is logical to assume that other mammals also are influenced by MHC characteristics during mate choice. Typically, individuals choose mates to reduce the likelihood of homozygous offspring but there is no reported preference or avoidance of specific MHC haplotypes (Wedekind et al. 1995, Ober et al. 1997). Picking a mate according to MHC haplotype not only has significant effects on polymorphism (Jordan and Bruford 1998), but also reduces the likelihood of prenatal mortality and longer intergestational periods (Fadao et al. 2002). Studies on mice in particular have found that both male and female mate choice are affected by MHC preference (Eklund 1997). Additionally, there is evidence in mice and humans that MHC preference is based on parental MHC haplotype and not the MHC haplotype of the individual; specifically, the preference in humans is to find a mate dissimilar to the parents' MHC genotypes (Ober et al. 1997). Wedekind et al. (1995) also found that women who are not pregnant and not using oral contraceptives (which mimic pregnancy hormones) preferred men with MHC haplotypes dissimilar to their own.

Ditchkoff et al. (2001c) found that MHC heterozygosity in white-tailed bucks was an honest signal of quality and was associated positively with greater age-adjusted antler development, body mass and skull length, and testosterone levels. Because MHC heterozygosity is an honest signal of quality in white-tailed deer, it is possible that mate choice is influenced by MHC haplotype both as a method of finding high-quality mates and as a method of inbreeding avoidance.

Effects of Social Structure on Kin Recognition and Inbreeding Avoidance

Inbreeding avoidance mechanisms are not universal to all animals; the potential effects of inbreeding depression must be severe enough that there would be an evolutionary advantage for kin recognition and inbreeding avoidance. Additionally, the social system must be one where kin are likely to encounter one another after maturity so that there is an opportunity for inbreeding to occur (Pusey and Wolf 1996). Kin recognition is dependent on comparing potential mates to a standard and the development of the standard relies on the social structure of the species. In species where individuals are likely to encounter siblings later in life, familiarity may evolve so that individuals can recognize those they were raised with as kin (Pusey and Wolf 1996) such as in the striped mouse (Pillay 2002). If a species has a less rigid social structure where relatives may or may not encounter each other, that species may evolve phenotype matching based on parental or personal phenotypes so that unfamiliar relatives will still be recognized as kin (Pusey and Wolf 1996) as in the mandarin vole (Fadao et al. 2002). Additionally, the degree of kin recognition is dependent on the species' social structure, thus allowing mate choice to be dependent on factors other than those such as dominance rank (Paterson and Pemberton 1997). Some species, such as Japanese quail (*Coturnix coturnix*) may also have a preference for intermediate relatives to avoid out-breeding and to ensure that mates come from the same species (Bateson 1982).

The two mechanisms of kin recognition may both be present in a single species if the social structure of the species is such that both are beneficial. For example, Fadao et al. (2002) found that both familiarity and phenotype matching are at work in mandarin voles, a species where litters do not typically mix in low density situations but can mix in high density situations. It is beneficial for mandarin voles to have kin recognition by familiarity in low-density situations but kin recognition by phenotype matching is beneficial in high-density situations.

Though a species may have the potential for kin recognition and avoidance (e.g., by MHC phenotype matching), their social system may also be such that there is no need for inbreeding avoidance mechanisms. For example, Holand et al. (2007) studied reindeer in a harem-based mating system and found no evidence of inbreeding avoidance. The genetic analysis pointed to random mating with regards to genetic relatedness, though females preferred dominant males. Because reindeer are traditionally migratory, there would have been a great deal of gene flow as individuals travelled and associated with unrelated individuals, and there would have been little evolutionary pressure to develop behavioral inbreeding avoidance mechanisms. Furthermore, a study on wood bison (*Bison bison athabascae*) found no evidence of inbreeding avoidance as a genetic analysis indicated random mating (Wilson et al. 2002). Wilson et al. (2002) hypothesized that the fluidity of herd membership coupled with the great distances covered by herds reduced the likelihood of two related individuals mating. Therefore, although a species has the potential to exhibit inbreeding avoidance mechanisms based on phenotype matching or familiarity their social structure may be such that they have not developed such avoidance behaviors.

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II. Evaluation of Reproductive Behavior in White-tailed Deer through Genetic Parentage Analysis

Chapter Summary

Relatively few studies have utilized genetic technology to examine reproductive behavior in white-tailed deer through parentage analysis resulting in gaps in knowledge of reproductive behavior in white-tailed deer. This study examined relationships between reproductive success in male white-tailed deer and body size, age, and antler characteristics, age-related mate choice, and inbreeding avoidance using genetic parentage assignment. Between December 2007 and August 2010, 115 deer from inside a 174-ha high-fence facility in Alabama were captured and subsequently genotyped at 14 DNA microsatellite loci. Capture efforts included attempting to capture each deer inside the facility every year to collect data on body size and antler characteristics. Fifty-four paternities and 48 maternities were assigned using the program CERVUS. No relationships were detected between male reproductive success, body size, and antler characteristics. However, prime-aged males were more likely to breed and sired more offspring on average than younger males. Three cases of multiple paternity were observed including the first reported triplet multiple paternity with three sires. Evidence of age-related mate choice was identified but no evidence of inbreeding avoidance behaviors was found. A greater understanding of the physical factors that influence

reproductive success in male white-tailed deer will be beneficial for management purposes and in understanding the reproductive ecology of a cryptic species.

Introduction

In all animals, the urge to reproduce drives and shapes their behavior and ecology. For that reason, a major area of ecological research for most species focuses on reproduction. By thoroughly understanding reproduction in a species, we are then able to understand the interactions and consequences of mate selection, evolution, intersexual signaling, fitness, etc. Surprisingly, very little is known about some aspects of reproduction in white-tailed deer (*Odocoileus virginianus*) despite their status as one of the most-studied free-ranging species on the planet (Halls 1984, Hiller 1996, Geist 1998, Demarais et al. 2000). There are extensive data sets on litter size, gestation, growth rates, and other easily quantifiable aspects of reproduction (Hayssen et al. 1993). However, our understanding of some aspects of the reproductive ecology of the two sexes is limited. For example, little is known about how antler development influences male reproductive success, whether inbreeding avoidance behaviors are utilized, and to what degree female choice influences reproduction. Because the white-tailed deer is the most economically important game species in North America, being hunted by 10.1 million hunters over 132 million days in 2006 (USFWS 2006), complex population models based on reproductive data have been developed for use by land owners and managers (e.g., Fuller 1990, Xie et al. 1999). Some landowners and managers commonly implement complex harvest prescriptions (e.g., harvesting certain individuals or age classes) designed to improve the genetic composition of local herds and promote breeding success of particular bucks.

Furthermore, many management prescriptions, strategies, and decisions are based on assumptions of breeding success of which very little is known (Miller and Marchinton 1995, Rollins 1998, Carpenter 2000, Demarais et al. 2000, Harris et al. 2002).

The cryptic nature and large home range of deer makes free-ranging observations difficult so the majority of reproductive knowledge to date has been gathered from studies using captive deer in pens, limited research based on behavioral observations of wild white-tailed deer populations, or hunter-harvested deer. Multiple studies on white-tailed deer, both in penned and free-ranging studies, have documented greater reproductive success in prime-aged bucks than in yearling bucks (Jacobson 1992, Miller and Ozoga 1997, Sorin 2004, DeYoung et al. 2009a). In addition, body size in male white-tailed deer has been associated positively with male dominance status (Townsend and Bailey 1981, DeYoung et al. 2006), and male dominance associated positively with reproductive success (DeYoung et al. 2006). Though captive deer have provided a starting point in studying white-tailed deer reproduction, the small size of captive pens, artificial age and sex structures commonly found in captive populations, and forced nature of social interactions cast doubt on whether penned animals can be used to effectively examine some factors of breeding ecology in white-tailed deer (e.g., how physical characteristics influence male reproductive success). For these reasons, data from related species and species with similar reproductive systems have been the basis for predictions of aspects of white-tailed deer breeding ecology such as how physical characteristics influence male reproductive success.

Though prime-aged, large-bodied, and more ornamented males are considered the most reproductively successful in ungulate species (red deer, *Cervus elaphus*: Kruuk et al. 2002; Soay sheep, *Ovis aries*: Preston et al. 2003), they do not completely exclude other males from breeding opportunities (white-tailed deer: Jacobson 1992, Miller and Ozoga 1997, Sorin 2004, DeYoung et al. 2006, 2009a; red deer: Kruuk et al. 2002; Soay sheep: Preston et al. 2003). Additionally, individual breeding success varies greatly between years, suggesting that male breeding success is dynamic and individual males may be unable to dominate breeding through consecutive years (Mathews and Porter 1993). In a penned study with white-tailed deer by DeYoung et al. (2006), though prime-aged males were dominant, dominance ranks were not stable throughout the duration of the study. In particular, males older than 3 years of age had only a weak association between age and dominance, while there was a strong association between age and dominance for males younger than 3 years of age (DeYoung et al. 2006). Sorin (2004) focused exclusively on assigning paternities in a simulated, free-ranging, white-tailed deer population and discovered that males from all ages >0.5 years of age were reproductively successful and that multiple paternities occurred in 22% of compound litters. Multiple paternities likely indicate that a single male cannot monopolize breeding opportunities and that even a male who has successfully bred with a doe cannot completely exclude other males from mating with her. DeYoung et al. (2009a) reported that all male age classes >0.5 years of age sired offspring in 3 free-ranging populations. A single dominant prime-aged male could not monopolize multiple estrous females in captivity, as multiple paternities also occurred when multiple does were in estrous (DeYoung et al. 2009b).

Whereas these studies advanced our understanding of reproductive patterns in white-tailed deer considerably and identified previously unknown breeding characteristics (e.g., multiple paternities), they did not explore how factors (e.g., body size, antler size) other than age influence reproductive success or address whether inbreeding avoidance and mate selection occurred. Additionally, detailed knowledge of every individual in an open population is practically impossible, therefore limiting the ability of researches to examine an individual male's reproductive success over time. In this study, we examined a population of white-tailed deer in a 174-ha high fence enclosure that simulated the behavior of a free-ranging population. Because it was an enclosed population, we were able to follow the same individuals in the population over time and incorporate data on physical characteristics and development into our analyses. The specific objectives of this study were to: (1) examine relationships between reproductive success and age, body size, and antler characteristics in male white-tailed deer, (2) investigate whether age-related mate choice may be occurring, and (3) provide a cursory examination of whether white-tailed deer engage in inbreeding avoidance.

Methods

Study Area

The Auburn University Deer Lab was located at the 566-ha Piedmont Substation of the Alabama Agricultural Experiment Station in Camp Hill, Alabama. Our study population was located within a 174-ha high-fence enclosure surrounded by a 2.5-m, high-tensile, deer proof fence. The study population consisted of deer that were within the study area when the facility was constructed in October 2007. The facility was located in the Piedmont physiographic region and was composed of approximately 50% pasture that was maintained for hay production and was cut twice each year.

Approximately 15% of the study area was composed of bottomland hardwoods and another 15% was composed of upland hardwood-pine (*Pinus* spp.) mix. An estimated 10% of the study area was composed of 10 - 15 year old planted loblolly pine (*Pinus taeda*) and the remaining 10% was composed of early pine regeneration and scrub. Also included within the study area were 2 0.81-ha food plots where agronomic research into the feeding preferences of the study population was being conducted. Food plots were planted with a variety of forage crops including, but not limited to, alfalfa (*Medicago sativa* L.), clover (*Trifolium spp*), corn (*Zea mays* L.), wheat (*Tricum aestivum* L.), and soybean (*Glycine max* L. Merr.). Three feeders were located in the study area and supplied an 18%-protein, pelleted deer feed (Biologic Deer Feed by SouthFresh Feeds, Demopolis, AL) ad libitum as the population density within the enclosure was greater than the natural carrying capacity of the area. Nutritional supplement pellets were provided year-round in the feeders.

Capture and Handling

Every year beginning in 2009, a camera survey of the deer population was performed after the breeding season to estimate minimum and maximum population densities for bucks, does, and fawns and to aid in identifying which captured deer were still alive. White-tailed deer were captured within the study area during December 2007 through March in 2009 and 2010 in a manner similar to that described by Kilpatrick and Spohr (1999) using an intramuscular injection of telazol (250 mg) and xylazine (200mg) delivered with dart guns over prebaited sites. We also captured deer using a capture facility, a permanent capture corral. The capture facility was composed of a fenced-in, 0.69-ha field with a gate at one corner and a wooden hallway and sorting boxes on the other. Separating the field and the hallway was a door that could be dropped vertically using black-powder charges triggered with a remote blasting box. Deer in the hallway were moved into individual containment boxes and sedated with 125 mg/45.36 kg telazol and 100 mg/45.36 kg xylazine prior to data collection. Upon completion of data collection, all deer were given an intramuscular injection of 100 mg/45.36 kg tolazine to reverse sedation.

Data Collection

We measured skull length, body length, hind foot length, tail length, and chest girth on all captured deer using a flexible measuring tape approximately 1 cm in width. Skull length was obtained by measuring the distance from the tip of the snout to the posterior of the sagittal crest. Body length was measured as the dorsal distance from the tip of the snout to the base of the tail. Hind foot length was measured as the distance from the tip of the hoof to the posterior end of the tuber calcis. Tail length was measured as the distance from the tip of the tail bone to the base of the tail. Chest girth was measured as the circumference of the chest immediately posterior to the front legs. Male deer had their antlers measured according the Boone and Crockett scoring system (Wright et al. 2003) and all deer were aged by tooth wear and replacement (Severinghaus 1949). While deer were anesthetized, a 1-cm^2 ear notch was collected and frozen for genetic analysis for parentage assignment.

Two different ear tags were attached to each captured deer. The left ear received a color-coded ear tag indicating the year of capture and an individual identification number. Deer identification numbers included the birth year and the unique identification of that deer within its cohort (e.g., deer 705 was born in 2007 and was the fifth deer caught from that birth year). We placed a white ear tag also containing the individual identification number for that deer in the right ear. The year of birth was freeze-branded using metal branding irons on the shoulder and the individual's cohort number on the hip (e.g., deer 705 had a 7 on each shoulder and 5 on each hip) using the technique described by Newsom and Sullivan (1968). Freeze-branding kills the melanocytes in the hair follicles exposed to the brand resulting in the hair on the brand site growing back white (Newsom and Sullivan 1968).

Genetic and Data Analysis

Genetic analysis was conducted by an outside source (DNA Solutions, Inc., Oklahoma City, OK) using microsatellite analysis of 14 loci. The resulting allelic markers were entered into CERVUS 3.0 (Kalinowski et al. 2007) to assign parentage through the use of likelihood ratios, estimate the level of confidence of parentage assignments, and determine if the population was under Hardy-Weinberg equilibrium. Once parentage was assigned, we used a Poisson regression model in the statistical program R (R Development Core Team 2008) to examine relationships between male reproductive success and age, antler characteristics, and body size. Only paternities attributed to sires with antler and body measurements during the corresponding breeding season were included, and all variables were treated as continuous. We included the effect of individual in the regression as a random effect to account for differences in number of data points per individual.

In addition to this regression analysis, we also grouped paternities by year and sire age class. After doing so, we used logistic regression to compare the likelihood that a buck that was 0.5, 1.5, 2.5, and 3.5 years of age would sire offspring. Bucks 4.5 and 5.5 years of age were excluded from the logistic regression because they always sired offspring. A Poisson regression was used to compare the average number of offspring per sire for each age class except 5.5 years of age, as there was only one individual that was 5.5 years of age during the study. The second Poisson regression had greater sample size because only age was included as a categorical variable and all sires had age data available.

The average absolute distance in parental age was calculated using cases where CERVUS was able to assign both parents to an individual. We compared the average with a non-parametric distribution created by plotting absolute average distances from 1,000 iterations of random potential parent combination to test for significant deviation from parental age distances resulting from random mating. A pedigree of individuals involved in the CERVUS parentage results was constructed using PEDIGRAPH 2.4 (Garbe and Da 2008) and modified in Inkscape 0.48 (http://inkscape.org/).

Results

A total of 115 deer, 67 females and 51 males, were sampled between December 2007 and August 2010 and subsequently genotyped. Beginning in 2009, most individuals captured for the first time were of known age (i.e., 1.5 years of age or younger), and 76 of the 115 deer sampled were of known age. Population density as estimated by camera survey was approximately 0.36 deer/ha when the facility was first constructed in 2007 and peaked at 0.46 deer/ha in 2009 (Table 2.1). The ratio of adult does to adult bucks was 2:1 when the facility was first constructed and was approximately 1:1 by 2010. At the beginning of the study in 2007, the oldest bucks observed were 2.5 years old with the majority of known males being fawns (Table 2.2). By 2010, the oldest buck was 5.5 years old and an additional 18 bucks were between 2.5 and 3.5 years old. Approximately 24% of the reproductive population was sampled in 2007 and increased to 82% by 2010. Sires were assigned to 55 individuals with 95% confidence, estimated exclusion probabilities >0.99, and ≤2 mismatches, though only 54 of the paternities occurred during the study period and were included in analyses. The excluded paternity was for an offspring born in 2006 and was excluded because it was the only individual in its cohort with paternity information. Dams were assigned to 48 individuals, and all but 1 had sires assigned to them as well. Three instances of multiple paternities were observed of the 9 compound litters indicated by CERVUS; of those, 2 were twin sets born in 2010 and 1 was a set of triplets with 3 different sires born in 2008. In 2007, the majority of offspring assigned paternity were sired by fawns, but in all subsequent years fawns sired only a small fraction of the offspring assigned paternity (Table 2.3).

We back-calculated the age of all sires at the time of breeding. However, of the 54 sires identified only 16 had chest girth and antler measurements for the relevant breeding season and could be included in the full Poisson regression. No relationship ($P > 0.05$) existed between reproductive success and age ($P = 0.848$), body size ($P = 0.643$), or antler size ($P = 0.730$; Table 2.4).

All 54 sires identified during the paternity analysis were included in the logistic regression and the Poisson regression comparing the average number of offspring sired by age class. There was no difference in the likelihood of bucks that were 1.5 and 2.5 years of age siring offspring compared to bucks 3.5 years of age (*P* = 0.171 and *P* = 0.127, respectively; Table 2.5). Bucks 3.5 years-old were 3.919 times as likely as 0.5 year-old bucks to sire offspring (*P* = 0.093). Bucks 4.5 years of age sired more offspring than bucks 0.5 years of age (*P* = 0.032), 1.5 years of age (*P* = 0.076), and 2.5 years of age (*P* = 0.072; Table 2.6). There was no difference (*P* = 0.207) in the average number of offspring sired by 3.5 and 4.5 year-old bucks.

Average absolute distance in parental ages observed (1.826) differed from random parent pair combinations (*P* = 0.032). Dams produced offspring more often with sires 3 years younger and less often with sires 2 years younger than if random mating was occurring (e.g., if no mate preference is exhibited and every male has an equal probability of mating with a female; Figure 2.1). In addition, no offspring were produced by dams 4 years older than the sires.

A total of 89 individuals were included in the pedigree and all but 2 were linked to the rest through mating events (Figures 2.2, 2.3, 2.4). There was one instance of a father siring offspring with his daughter two different years and an instance of a mother producing a fawn with her son. In addition, one male was able to sire offspring with 9 different females over the course of the study, while the largest number of males that a single female produced offspring with was 4.

Discussion

Age is a trait that tends to be associated positively with male reproductive success. Our data supported conclusions of previous studies (Sorin 2004, DeYoung et al.

2006, 2009a) in that reproductive success of males was associated positively with age. Males 3.5 years of age were more likely to sire offspring than fawns, and males 4.5 and 5.5 years of age always sired offspring. In addition, the mean number of offspring produced by each 4.5 year-old sire was greater than the mean number of offspring produced by 0.5, 1.5, and 2.5 year-old sires (Table 2.6). Prime-aged bucks (3.5 and 4.5 years old) were likely able to sire more offspring than younger individuals because they were able to secure more breeding opportunities. Multiple studies on white-tailed deer have documented greater reproductive success in prime-aged bucks than in yearling bucks (Jacobson 1992, Miller and Ozoga 1997, Sorin 2004, DeYoung et al. 2009a). With age comes sexual, physical, and social maturity, all important aspects that allow males to be dominant and reproductively competitive. Physical maturity results in increased body size and more prominent and ornate ornamentation used as a secondary sexual characteristic (Demarais et al. 2000). By 3.5 years of age, bucks have reached physical maturity and are able to effectively compete with older males for dominance (Townsend and Bailey 1981, DeYoung et al. 2006) which in turn allows them to displace subordinate males from receptive does. Age also is associated positively with reproductive hormones, such as testosterone (Miller et al. 1987, Ditchkoff et a. 2001d), that tend to increase male aggressiveness (Lincoln et al. 1972, Miller et al. 1987).

Our dataset did not have sufficient sample sizes to adequately assess relationships between reproductive success, body size, and antler characteristics. Though our data was not able to support positive correlations between body size, antler characteristics, and reproductive success, other studies have documented relationships between reproductive success and physical characteristics. DeYoung et al. (2006) and Townsend and Bailey

(1981) reported that in penned white-tailed deer, the heaviest males were the most dominant, regardless of age, and were the most reproductively successful. Male red deer also exhibit a positive correlation between body size and reproductive success which has been attributed to fighting success (Clutton-Brock et al. 1979). Increased reproductive success in highly ornamented males has not been documented in white-tailed deer but has been documented in other mammalian species. Southern mule deer males (*Odocoileus hemionus fuliginatus*) with larger antlers were more dominant, more likely to engage in courtship behaviors, and were the only males observed to copulate with females (Bowyer 1986). Kruuk et al. (2002) found that antler mass in red deer was associated positively with annual breeding success, and lifetime average antler mass was associated positively with total lifetime breeding success. In addition, Malo et al. (2005) found that large-antlered red deer males had greater testes size and sperm velocity, suggesting that they were more reproductively competitive. Preston et al. (2003) also found a positive relationship between horn length and paternity success in male Soay sheep.

Annual patterns of breeding success in our study support the idea that older males may suppress breeding success of younger males. Between 2007 and 2009, a decline in the number of offspring sired by bucks younger than 3.5 years of age occurred regardless of the majority of bucks falling into the younger age classes. During the same time period, the oldest cohort of bucks reached 3.5 and 4.5 years of age and sired proportionally more offspring per sire than the younger age classes. This suggests that bucks 3.5 and 4.5 years old may have been able to suppress the reproductive success of younger bucks. Suppression of breeding effort in young white-tailed deer has previously been theorized to occur based on activity and movement patterns (Ozoga and Verme

1985, Miller and Ozoga 1997, Holtfreter 2008). Ozoga and Verme (1985) found that yearling bucks were less active during the breeding season and exhibited less courtship behavior than older bucks. In addition to reduced activity levels during the breeding season itself, Holtfreter (2008) documented greater juvenile (1.5-2.5 years old) movement, mean movement rates, and path tortuosity during the pre-rut and suggested that juveniles focused their breeding efforts during periods when mature bucks are less active in the hopes of encountering does that come into estrous early. Rather than compete with older, more experienced males, juvenile reproductive effort was suppressed during the rut when mature males were expending effort toward breeding.

Suppression of breeding effort in young males has also been documented in red deer (Pemberton et al. 1992). During the rut, young red deer males experienced minimal weight loss compared to prime-aged males because they expended less reproductive effort, did not rut as long, and relied on the “sneaker” method that is less energetically costly than harem-holding (Yoccoz et al. 2002). This study also hypothesized that prime-aged males put the most effort into the rut because they would be the most successful, whereas younger males expended less effort because they would most likely be less successful. Along the same lines, Ditchkoff et al. (2001b) found that younger male white-tailed deer have reduced risk of natural mortality during and after the breeding season compared to mature males in populations with a significant proportion of mature males. They hypothesized that younger males were exerting less effort towards reproduction due to their reduced probability of success.

Our observed rate of multiple paternities (33.3%) was slightly greater than rates reported by Deyoung et al. (~25%; 2009b) and Sorin (22%; 2004). One set of multiple paternities occurred when 3.5 and 4.5 year-old bucks both successfully bred with a 5.5 year-old doe, another when 2.5 and 4.5 year-old bucks bred with a 3.5 year-old doe, and the last set of multiple paternities occurred when three yearling bucks bred a 5.5 year-old doe and produced triplets. Although alternative mating strategies such as sneaking can account for multiple paternities, as seen in red deer (Clutton-Brock et al. 1982), current knowledge of white-tailed deer breeding behavior suggests that this is not the case. Once a male finds an estrus doe, he follows her, mates with her, and tends her for an extended period of time, reducing the chances of other males mating with and fertilizing that doe. If confronted by a more dominant male at any point during the courtship, he will be displaced by the dominant buck. Therefore, as hypothesized by Sorin (2004) and Deyoung et al. (2009b), it is more likely that multiple paternity occurs when a subordinate buck is displaced by a dominant buck. In the case of the triplet multiple paternity, it may be that there was no clear dominance hierarchy between the three yearlings, and they were able to displace each other without any clear physical factors that could predict dominance.

Female mate selection has not been definitively documented in white-tailed deer, though males have potential signals of mate quality, including antler symmetry (Ditchkoff et al. 2001a, Ditchkoff et al. 2001c), scent marks from forehead rubs (Atkeson and Marchinton 1982, Gassett et al. 1997), scent marks from rub-urination (Miller et al. 1998), and interdigital scent glands (Gassett et al. 1996). The closest documentation of female mate choice in white-tailed deer were the observations by Ozoga and Verme (1985) that yearling does occasionally behave as if intimidated by mature bucks and flee before copulation can occur. In addition, they observed that mature does often act aggressively toward yearling bucks, regardless of whether the buck was attempting to court the doe. Yearling does also were more likely to be bred by yearling bucks (Ozoga and Verme 1985). In our study population, females tended to mate with males that were younger than themselves. Specifically, a greater percentage of matings occurred between females 3 years older than the male than would have been expected if random mating had occurred. Assuming that the study population exhibited similar behaviors as those observed by Ozoga and Verme (1985), it is unlikely that does were selecting for mates based on age, as the bucks involved in matings where the doe was 3 years older were primarily fawns and yearlings. One explanation is that does were selecting mates based on a factor other than age (genetic distance, genetic quality, etc.), and the desired bucks were 3 years younger. An alternate explanation would be that female mate choice was not occurring and yearling and fawn bucks were able to mate with receptive does because of the low availability of mature bucks during the early years of the study. Additionally, because fawns are still part of the mother's social group and yearling males may not have dispersed yet or are more readily accepted into doe social groups (Ozoga and Verme 1985), it is possible that they were able to take advantage of receptive does in the absence of mature males.

We found no support for the practice of inbreeding avoidance in white-tailed deer, as the interconnectedness of 87 of the 89 individuals in the pedigree and the occurrence of parent-offspring matings suggested that white-tailed deer did not practice inbreeding avoidance. In addition, it is possible that the 2 individuals that are not linked with the remainder of the population in our constructed pedigree could have been linked, but the link was not detected because only a sire was assigned for the offspring in question and the dam may be linked into the pedigree through matings with some of the males included. As more generations are produced, the pedigree will likely become increasingly convoluted as cousins and half-siblings become more reproductively active. Inbreeding avoidance can be important for species because inbreeding can begin to have a negative effect on the fitness of inbred individuals (e.g., inbreeding depression) over time, typically resulting in increased mortality of young and adults and reduced reproductive capability in surviving adults (Chen 1993, Jimènez et al. 1994, Slate et al. 2000).

White-tailed deer have the ability to practice inbreeding avoidance by selecting mates based on major histocompatibility complex (MHC) genes that influence immune function (Bjorkman and Parham 1990), as buck antlers are honest indicators of MHC quality (Ditchkoff et al. 2001c). The MHC has been documented as affecting mate selection in a number of species including humans (*Homo sapiens*: Wedekind et al. 1995, Ober et al. 1997), ring-necked pheasants (*Phasianus colchicus*: von Schantz et al. 1996), and mice (*Mus domesticus*: Beauchamp et al. 1988, Eklund 1997), and it is logical to assume that other mammals also are influenced by MHC during mate choice. However, the capacity for inbreeding avoidance does not necessitate the practice of inbreeding avoidance as reindeer (*Rangifer tarandus*; Wilson et al. 2002) and wood bison (*Bison bison athabascae*; Holand et al. 2007) exhibit no inbreeding avoidance despite having the same potential avoidance mechanisms as white-tailed. The lack of inbreeding avoidance these populations was hypothesized to be the result of historic migratory lifestyles in which constant gene flow between populations occurred and compensated for inbreeding. If white-tailed deer do not practice inbreeding avoidance, the promiscuity of both sexes may counteract inbreeding, as both sexes mate with many different partners thus producing offspring with various levels of genetic diversity. In addition, the ability of yearling bucks to disperse long distances (Nixon et al. 1991, Hölzenbein and Marchinton 1992, Long et al. 2005) may guarantee constant gene flow with a more diverse meta-population.

This study did not measure true reproductive success, but instead used recruitment as an approximation for reproductive success. Because fawns were not captured until they were at least 6 months of age, there may have been considerable numbers of fawns that died from natural causes (predation, disease, condition, etc.) prior to capture. This approach to estimating reproductive success is similar to that taken by Sorin (2004) and Deyoung et al. (2009a). In order to measure actual reproductive success, each breeding event needs to be recorded, and whether the offspring survive to adulthood or not. Due to the difficulty of behavioral observations on free-ranging white-tailed deer, recruitment has been the only available metric for approximating reproductive success to date. In reality, true reproductive success is likely greater for all age groups because recruitment includes the effects of high fawn mortality rates (Cook et al. 1971, Nelson and Mech 1986, Vreeland et al. 2004, Saalfeld and Ditchkoff 2007). Future studies should consider the use of vaginal implant transmitters (Carstensen et al. 2003) to more accurately assess patterns of breeding and breeding success in cryptic species such as white-tailed deer.

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Table 2.1. Number of marked individual deer and minimum population estimates by group (i.e., buck, doe, fawn, total) by year, Auburn University Deer Lab, Camp Hill, AL, 2008-2011.

	Bucks		Does		Fawns		Total	
Year[a]	Marked[b]	Estimate[c]	Marked[b]	Estimate[c]	Marked[b]	Estimate[c]	Marked[b]	Estimate[c]
2008	1	14	9	28	3	22	13	64
2009	13	22	9	32	2	26	24	80
2010	28	30	18	31	7	19	53	80
2011	36	37	24	36	1	13[d]	61	86

[a] Abundances of tagged animals and population estimates are reflective of the population on March 1 of the corresponding year.

[b] Abundances of animals previously marked and considered live. Animals must be observed visually in the field or by trail camera during the previous 12 month period or at any point following the census period to be considered live.

[c] Population estimates for 2011 determined using information from trail cameras. Individual rates of detectability were determined for each deer group, and ratio of marked deer; unmarked deer and individual detectability rates were using in conjunction to generate population estimates. Estimates for previous years determined using population reconstruction.

[d] Fawn abundance was estimated during this year using adult doe abundance and recruitment rate from the previous year (i.e., 0.7 fawns/doe) due to the low number of marked fawns in the population. This estimate accounts for total recruited fawns minus fawns removed from the population.

Table 2.2. Number of sampled bucks by age class available to sire offspring, Auburn University Deer Lab, Camp Hill, AL, October 2007 - August 2010.

	Age class					
Year	0.5	1.5	2.5	3.5	4.5	5.5
2007	8	3	2	0	0	0
2008	9	8	3	2	0	0
2009	13	8	8	3	2	0
2010	3	10	8	7	3	1

Table 2.3. Number of sampled offspring sired by sire age class, Auburn University Deer Lab, Camp Hill, AL, October 2007 - August 2010.

	Age class					
Year	0.5	1.5	2.5	3.5	4.5	5.5
2007	4	1	0	0	0	0
2008	2	9	3	6	0	0
2009	1	1	3	3	7	0
2010*	1	0	1	5	6	1

*Incomplete sampling of fawns recruited in 2010 occurred due to completion of field work in August 2010.

Table 2.4. Estimates, standard errors, z-values, and P-values for paternal age, Boone and Crockett antler score, and chest girth resulting from a Poisson regression relative to number of fawns sired, Auburn University Deer Lab, Camp Hill, AL, October 2007 – August 2010.

	Estimate	S.E.	z- value	P
Intercept	-1.059	2.969	-0.356	0.721
Paternal Age	0.066	0.349	0.191	0.848
Paternal Antler	-0.004	0.012	-0.344	0.730
Paternal Chest	0.001	0.003	0.463	0.643

Table 2.5. Likelihood estimates of individual males (by age class) siring offspring, Auburn University Deer Lab, Camp Hill, AL, October 2007 - August 2010.

	Sire age class															
	0.5				1.5				2.5				3.5			
	Estimate ± S.E.	Likelihood	z value	P	Estimate ± S.E.	Likelihood	z value	P	Estimate ± S.E.	Likelihood	z value	P	Estimate ± S.E.	Likelihood	z value	P
0.5	0.134*															
1.5	0.252 ± 0.683	1.286	0.368	0.713	0.166*											
2.5	0.055 ± 0.766	1.057	0.073	0.942	-0.195 ± 0.766	0.822	-0.255	0.798	0.140*							
3.5	1.366 ± 0.813	3.919	1.679	0.093	1.114 ± 0.813	3.047	1.369	0.171	1.310 ± 0.858	3.706	1.526	0.127	0.377*			

*Absolute probability of sire age class siring offspring

Table 2.6. Estimates, standard errors, z-values, and P-values for male age classes resulting from a Poisson regression of the number of offspring sired by sampled sires of each age class, Auburn University Deer Lab, Camp Hill, AL, October 2007 – August 2010.

	Sire age class														
	0.5			1.5			2.5			3.5			4.5		
	Estimate ± S.E.	z value	P	Estimate ± S.E.	z value	P	Estimate ± S.E.	z value	P	Estimate ± S.E.	z value	P	Estimate ± S.E.	z value	P
0.5	1.285*														
1.5	0.200 ± 0.449	0.446	0.655	1.571*											
2.5	0.085 ± 0.504	0.169	0.866	-0.115 ± 0.483	-0.239	0.811	1.400*								
3.5	0.442 ± 0.427	1.034	0.301	0.241 ± 0.403	0.598	0.549	0.356 ± 0.463	0.770	0.441	2.000*					
4.5	0.927 ± 0.433	2.138	0.032	0.726 ± 0.409	1.774	0.076	0.842 ± 0.469	1.796	0.072	0.485 ± 0.385	1.260	0.207	3.250*		

*Average number of offspring produced per sire in sire age class

Figure 2.1. Observed age difference between dams and sires from 2007-2010, and predicted age differences between dams and sires assuming the occurrence of random mating, Auburn University Deer Lab, Camp Hill, AL.

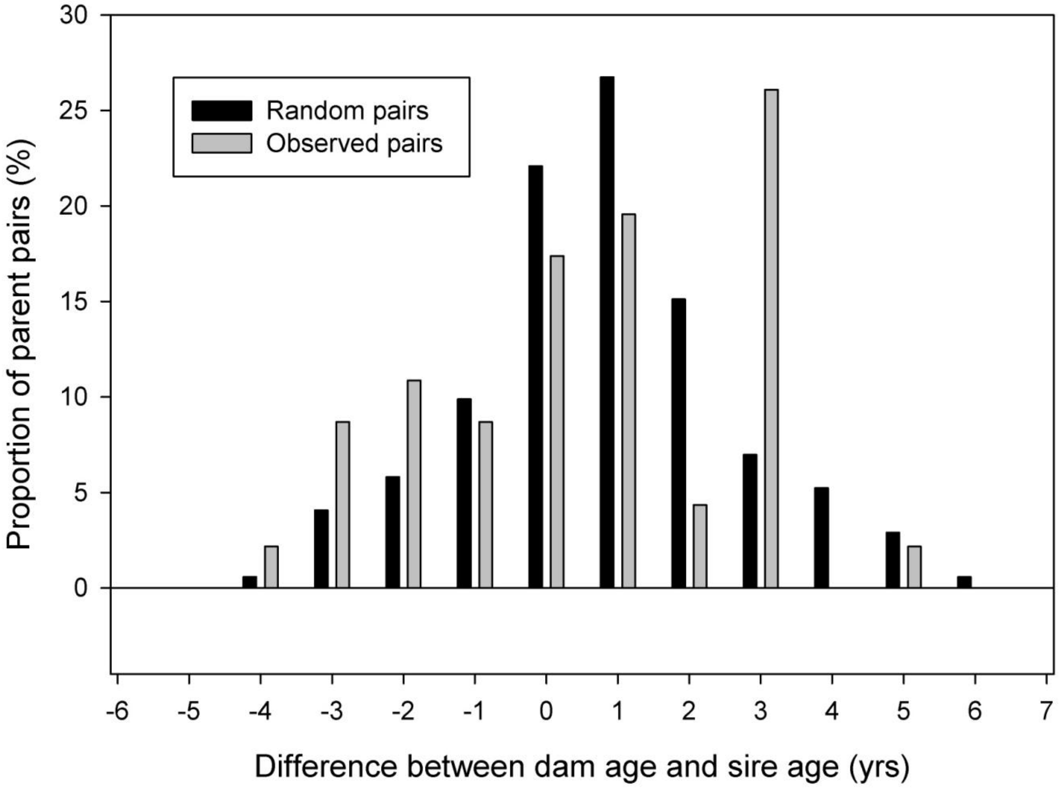

Figure 2.2. Complete pedigree of all individuals sampled from 2007-2010, Auburn University Deer Lab, Camp Hill, AL. Parentage assignments were constructed using CERVUS 3.0 and the pedigree using PEDIGRAPH 2.4. Lines that extend past the edge of the figure are identified by letters, and can be found continuing on Figure 2.3 by matching the letter identifiers.

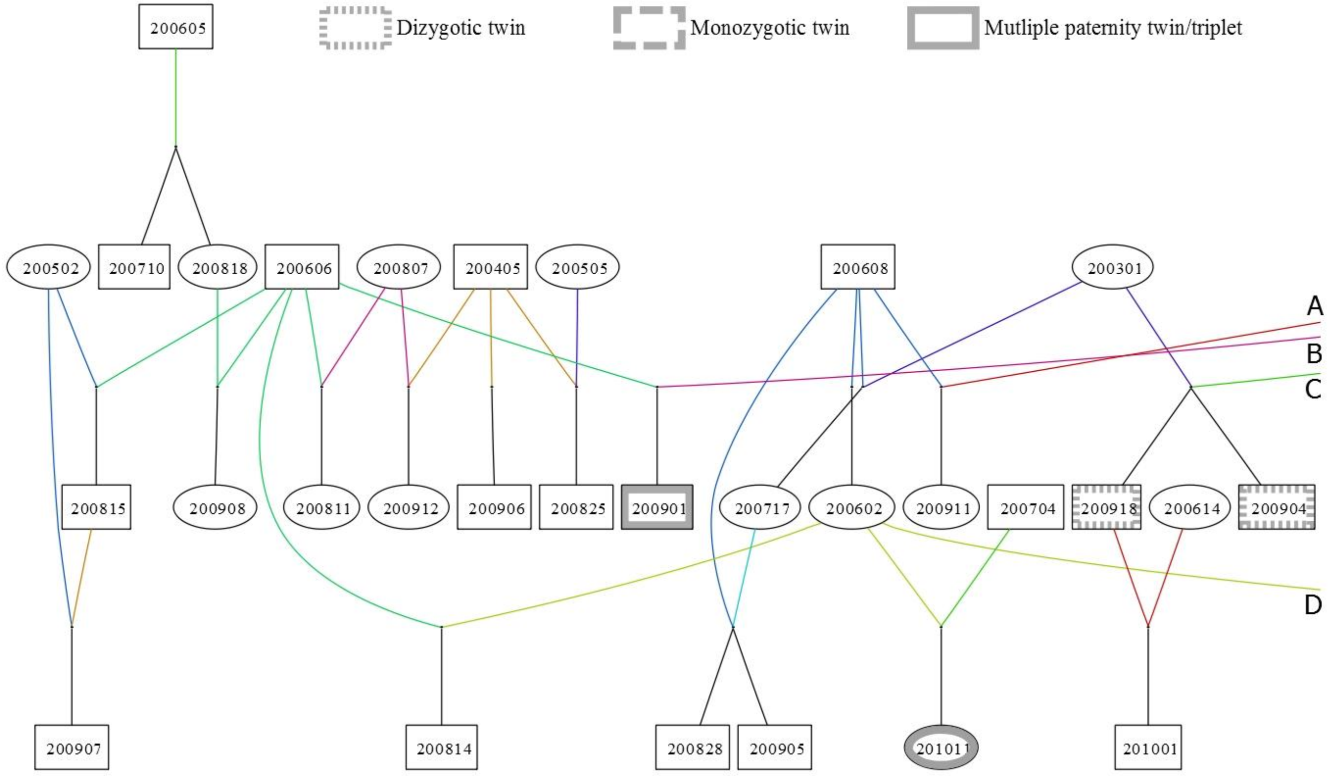

Figure 2.3. Complete pedigree of all individuals sampled from 2007-2010, Auburn University Deer Lab, Camp Hill, AL. Parentage assignments were constructed using CERVUS 3.0 and the pedigree using PEDIGRAPH 2.4. Lines that extend past the edge of the figure are identified by letters, and can be found continuing on Figure 2.2 and Figure 2.3 by matching the letter identifiers.

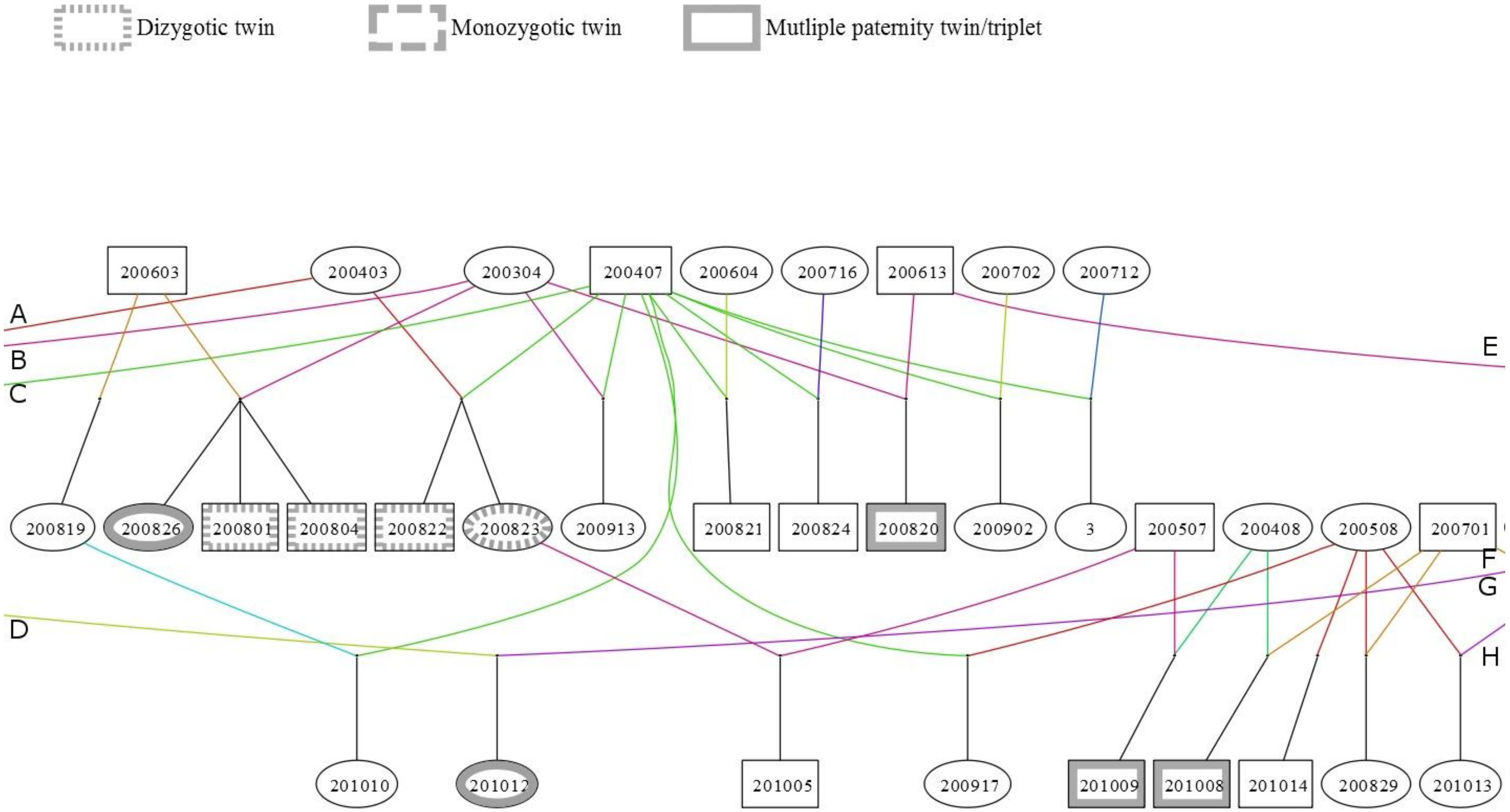

Figure 2.4. Complete pedigree of all individuals sampled from 2007-2010, Auburn University Deer Lab, Camp Hill, AL. Parentage assignments were constructed using CERVUS 3.0 and the pedigree using PEDIGRAPH 2.4. Lines that extend past the edge of the figure are identified by letters, and can be found continuing on Figure 2.3 by matching the letter identifiers.