

HONEST ADVERTISEMENT IN MALE WHITE-TAILED DEER:
EVIDENCE FOR THE HANDICAP HYPOTHESIS
OF MATE SELECTION

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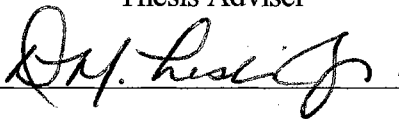
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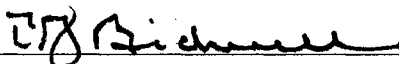
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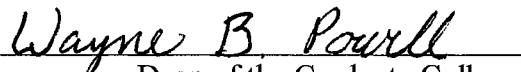


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NOMENCLATURE

ANCOVA	analysis of covariance
ANOVA	analysis of variance
FA	fluctuating asymmetry
McAAP	McAlester Army Ammunition Plant
MHC	major histocompatibility complex
<i>Mhc-DRB</i>	<i>DRB</i> region of the major histocompatibility complex
<i>Odvi-DRB</i>	major histocompatibility complex alleles specific to white-tailed deer
P_m	probability of mortality
RFA	relative fluctuating asymmetry

CHAPTER I

ANTLER CHARACTERISTICS IN WHITE-TAILED DEER FOLLOW PATTERNS PREDICTED FOR SEXUALLY SELECTED TRAITS

Summary

Evolution of antlers among Cervidae has provided an ideal model for the study of sexual selection. It has been hypothesized that secondary sexual characters that signal male quality should demonstrate a negative relationship between size of the trait and degree of fluctuating asymmetry because they are costly to produce. We collected morphometric and antler data from 343 white-tailed deer (*Odocoileus virginianus*) in Oklahoma to determine if measures of asymmetry of antlers follow patterns predicted for sexually-selected characters. Although absolute fluctuating asymmetry was not related to antler size, relative fluctuating asymmetry was related negatively to antler size, suggesting that antlers may be a reliable signal of the genetic quality of the bearer in white-tailed deer. Relative asymmetry of antlers was greatest in deer 1.5 years of age and was related negatively to age. Relative asymmetry was related negatively to antler size within all age classes, except deer ≥ 6.5 years of age, where a positive relationship was detected between relative asymmetry and antler score. Our data suggest that deer ≥ 6.5 years of age are near the upper threshold of antler development and thus may be exhibiting increased asymmetry due to nutritional stress. Relative asymmetry also was related negatively to carcass mass,

inside spread, skull length, and body length. A negative relationship between asymmetry of antlers and morphometric measurements suggests that antler asymmetry in white-tailed deer may be a reliable signal of genetic quality of the bearer. Relative fluctuating asymmetry of antlers followed the pattern predicted for traits that may be selected for by females.

Introduction

Antlers in Cervidae have evolved as both weapons used for intrasexual competition and ornaments of intra- and intersexual display (Geist 1998). Cervids that are solitary and territorial typically have short simple antlers that are used primarily as weapons in territorial defense (Putman 1988). However, more social species have evolved ornate antlers with greater branching and palmation. In addition to weapons, these complex antlers serve as advertisements during intrasexual and intersexual displays (Geist 1991). During intrasexual display, antler size (e.g., number of points, beam length, degree of palmation) helps to establish dominance hierarchies among male white-tailed deer (*Odocoileus virginianus*; Townsend & Bailey 1981; Miller et al. 1987), red deer (*Cervus elaphus*; Bartos & Hyanek 1983a, 1983b), fallow deer (*Dama dama*; Malyon & Healy 1994), and caribou (*Rangifer tarandus*; Bergerud 1973). However, little is known about what particular antler characteristics are important during intersexual displays.

Zahavi (1975) proposed that secondary sexual characters (e.g., antlers, ornate feathers, bright colors) in polygynous species aid in attracting mates and can be reliable signals of male quality. Because they are expensive to produce in terms of resource allocation (Ullrey 1983) and androgenic suppression of the immune system (Alexander &

Stimson 1988; Folstad et al. 1989), they may serve as a reliable signal of the genetic quality of the bearer. In essence, secondary sexual character development is predicted to advertise genetic quality through resource acquisition and allocation during a period of increased susceptibility to parasitism and disease. Females that select mates based on secondary sexual character development should confer a genetic advantage (e.g., parasite and disease resistance) to their offspring (Hamilton & Zuk 1982). However, studies of mate selection in avian species have had conflicting results, and the validity of the immunocompetence handicap hypothesis (Zahavi 1975; Hamilton & Zuk 1982) has recently been questioned. While increased development of secondary sexual characters has been found to be selected for in some avian species (Andersson 1982; Møller 1988; Barnard 1990; Petrie et al. 1990), there has been no relationship detected in others (McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Zuk et al. 1990; Wittzell 1991).

Møller (1993) proposed that fluctuating asymmetry may play a role in mate selection and lend support to the immunocompetence handicap hypothesis. Fluctuating asymmetry is a measure of deviation from perfect bilateral symmetry in development of morphological characters (Van Valen 1962) and results from an individual's inability to adequately cope with environmental stresses (parasites, disease, nutrition, climate, pollution, etc.) during development of characters that are normally symmetrical (Nilsson 1994). Fluctuating asymmetry increases as an individual's developmental ability is increasingly impaired by environmental stresses. As a result, fluctuating asymmetry might serve as an indicator of the level of stress experienced by an organism (Leary & Allendorf 1989) and the genetic quality of that individual in terms of its ability to eliminate or cope with stressors (Møller 1990; Thornhill & Sauer 1992; Min 1997). Møller and Thornhill

(1998) detected an overall negative relationship between degree of fluctuating asymmetry and likelihood of being selected as a mate in their review of previously published papers. These relationships have been found in widely differing taxonomic groups, including oribi (*Ourebia ourebi*; Arcese 1994), gemsbok (*Oryx gazella*; Møller et al. 1996), swordtail fish (*Xiphophorus cortezi*; Morris & Casey 1998), zebra finches (*Taeniopygia guttata*; Swaddle & Cuthill 1994), and scorpionflies (*Panorpa japonica*; Thornhill 1992).

Møller (1993) posits that patterns of fluctuating asymmetry can be used to identify those traits that are selected for by females. He stated that an inverse relationship between degree of fluctuating asymmetry and trait size would be evidence of a character that is important in sexual selection. Because secondary sexual characters are costly to produce, those individuals that produce the greatest ornamentation (i.e., greater allocation of resources) should represent higher quality individuals of the population and therefore should have relatively lower levels of fluctuating asymmetry (Markusson & Folstad 1997). In contrast, there should be a flat or U-shaped relationship between asymmetry and trait size if females do not select for that trait (Møller 1993). Solberg and Sæther (1993) further predicted that there should be an inverse relationship between degree of fluctuating asymmetry and age of the individual (Smith et al. 1982). As a cohort progresses through time, environmental selection pressures should serve to increase the average quality (e.g., disease resistance, predator avoidance, resource acquisition) of the cohort as inferior animals are selected against.

White-tailed deer, being a polygonous species with extravagant ornamentation, might be expected to exhibit mating characteristics consistent with the immunocompetence handicap hypothesis (e.g., females choose mates, antlers signal male

quality); however, little evidence currently exists that supports this contention. In fact, it has been argued that the main function of antlers is for combat (Goss 1983:106), and others have contended that New World (e.g., *Odocoileus* spp.) deer do not use an advertisement system during breeding (Geist 1981). Studies with red deer (Clutton-Brock et al. 1982; Gibson & Guinness 1980) found no evidence that females had strong preferences for particular males. In contrast, Geist (1998:132) proposed a role for antlers in intersexual advertisement, and Byers (1997) indicated that in American pronghorns (*Antilocapra americana*), a species that exhibits reproductive behaviors similar to white-tailed deer, females do assess male quality and use that information during mate selection. Because the intricate branching and geometry of white-tailed deer antlers suggests function beyond combat (e.g., advertisement), we attempted to gain insight into mating systems of white-tailed deer by investigating relationships between fluctuating asymmetry of antlers, size of antlers, and age in a population in which there was a large proportion ($\geq 55\%$; Ditchkoff et al. 2000) of mature males (≥ 3.5 years old). Our objectives were to determine if antler asymmetry decreased with age and if antler asymmetry was related negatively to antler size. These relationships have been suggested to be present in species where female mate choice occurs, and we hypothesized that if antlers are important cues to females during sexual selection, then antler traits should follow patterns predicted by Møller (1993) and Solberg and Sæther (1993).

Materials and Methods

Our study population consisted of white-tailed deer harvested by hunters or captured by drop-net at the McAlester Army Ammunition Plant (McAAP) in southeastern

Oklahoma. The McAAP has limited public access and is open to traditional archery hunting via lottery. About 1,500 hunters participate in the hunts annually and have an average success rate of 10.7% (Ditchkoff et al. 1996, 1997). Predominant vegetation types at McAAP are meadows of native prairie grass (*Andropogon virginicus*, *A. gerardii*, and *Schizachyrium scoparium*) bisected by brushy draws (*Ulmus alata*, *Symphoricarpos orbiculatus*, *Prunus angustifolia*, and *Diospyros virginiana*), oak (*Quercus nigra*, *Q. shumardii*) bottoms, and post oak (*Q. stellata*)-blackjack oak (*Q. marilandica*) uplands.

We collected data from hunter harvested deer during 1994-1996 ($n = 263$) and deer captured using drop-nets during December-January 1994-1996 ($n = 80$). Captured deer were measured and released after affixing a radiocollar for further study. Antlers were measured according to the scoring system (Boone and Crockett) described by Nesbitt and Wright (1981) to obtain an estimate of total antler development. Boone and Crockett score is a trophy scoring system where scores for each antler are summed together with the inside spread (greatest distance between the main beams) to obtain an overall estimate of antler development. This system measures length of each tine, length of the main beam, and circumferences around the main beam at the base of the antler (basal circumference) and between successive tines (not to exceed 4 circumferences for each antler). We did not include scores in the analysis for animals that had broken tines or main beams. We did not measure length of all tines during 1994 so we could not calculate antler scores during that year. We measured chest girth, skull length, right hind-foot length, body length, and tail length to the nearest 0.1 cm on each animal. Field-dressed carcass mass was measured to the nearest 0.5 kg on those deer harvested by hunters. Deer were aged by tooth wear and eruption (Severinghaus 1949)

Absolute asymmetry was calculated as the difference between measurements of the right and left antlers; relative asymmetry was calculated as absolute asymmetry divided by the larger antler. Relative fluctuating asymmetry adjusts absolute asymmetry measurements for the size of the trait. We tested for directional asymmetry (a consistent bias towards one side of the body; Palmer & Strobeck 1986) in antler development using a paired t-test. Absolute and relative fluctuating asymmetry measurements were calculated for antler score, number of points, main beam length, and basal circumference.

We used Pearson correlations to examine interrelationships between asymmetry measures of antler score, number of points, main-beam length, and basal circumference. Because measures of asymmetry in score were correlated positively with all other asymmetry measures ($0.23 \leq r \leq 0.55$; $P \leq 0.05$; Table 1) and score is the best index of overall antler size (Marchinton et al. 1995), all references to asymmetry measurements, unless otherwise stated, are for antler score. We tested for year and age effects on relative fluctuating asymmetry using 2-way analysis of variance. We compared variability of relative symmetry within age classes using Levene's test. We classified relative asymmetry measures into categories of low (<0.2), medium ($0.2-0.4$), and high (>0.4) and compared the frequency of observations in these categories among developmental age classes (1.5-2.5, 3.5-4.5, and ≥ 5.5 years of age) using Fisher's exact test. We used simple-linear regression to determine relationships between asymmetry (absolute and relative) and score of the larger antler rather than total or mean score of both antlers (Sullivan et al. 1993). We also used simple linear regression to determine relationships between asymmetry (absolute and relative) and gross Boone and Crockett score. We tested for relationships between morphometric measurements and asymmetry (absolute and relative) using

Pearson correlations. Individuals ≥ 6.5 years of age were grouped for age analyses due to inaccuracies in aging older animals (Jacobson & Reiner 1989) and the fact that antlers approach their greatest size from 6.5-7.5 years of age in white-tailed deer (Cook 1984). All analyses were performed using the Statistical Analysis System (SAS Institute Inc. 1990).

Results

Mean FA for the sampled population did not differ from zero ($P = 0.290$), indicating that there was no directional asymmetry. There was no difference in the magnitude of relative asymmetry in deer antlers among years ($P = 0.999$), but we did observe that 1.5 year-olds had greater ($P \leq 0.05$) relative fluctuating asymmetry than other age classes (Fig. 1). There was a negative relationship between relative fluctuating asymmetry (RFA) and age ($\text{RFA} = 0.054 + 0.330(1/\text{age}^2)$; $r^2 = 0.08$; $P < 0.001$; Fig. 2). In contrast, there was no age effect ($P = 0.513$) on absolute asymmetry of score. We found greater ($P < 0.01$) variability in relative asymmetry of 1.5-year old deer than other age classes. There was a greater ($P < 0.001$) frequency of deer with medium ($n = 24$) and high ($n = 16$) levels of relative asymmetry among deer ≤ 2.5 years of age compared with deer ≥ 3.5 years of age (medium, $n = 3$; high, $n = 1$). Relative asymmetry was related negatively to antler score ($\text{RFA} = 0.243 - 0.003(\text{score})$; $r^2 = 0.15$; $P < 0.001$; Fig. 3). This relationship also was negative ($P = 0.015$) for 3.5 year-old deer, but deer ≥ 6.5 years of age showed a positive relationship ($r^2 = 0.46$; $P = 0.032$) between relative asymmetry and antler score. There was no relationship ($r^2 = 0.02$; $P = 0.082$) between absolute asymmetry and size (antler score) of antlers. There was an overall negative relationship

between relative asymmetry and gross antler score ($RFA = 0.255 - 0.001(\text{score})$; $r^2 = 0.22$; $P < 0.001$; Fig. 3). This relationship held true for all age classes ($P \leq 0.05$), except for deer ≥ 6.5 years of age for which there was a positive relationship ($P = 0.028$; Fig 4).

Relative fluctuating asymmetry was correlated negatively with body mass ($r = -0.35$; $P < 0.001$), inside spread (greatest distance between the main beams; $r = -0.46$; $P < 0.001$), skull length ($r = -.019$; $P = 0.005$), and body length ($r = -0.28$; $P < 0.001$; Fig. 5). These relationships did not hold true ($P > 0.05$) within age classes with the following exceptions: 1.5-year old carcass mass ($r = -0.33$; $P = 0.009$), inside antler spread ($r = -0.37$; $P < 0.001$), and skull length ($r = -0.27$; $P = 0.14$); 2.5-year old spread ($r = -0.41$; $P = 0.001$); and 5.5-year old skull length ($r = 0.65$; $P = 0.032$). Carcass mass, gross Boone and Crockett score, main beam length, basal circumference, number of antler points, and inside spread increased with age ($P < 0.001$; Fig. 6).

Discussion

Relative asymmetry of antler scores in our study followed the pattern predicted by Møller (1993) of a secondary sexual trait that is selected for by females when choosing a mate. Møller (1993) indicated that a negative relationship between degree of asymmetry and size of a character occurs in characters that are selected for by females due to their reliability as honest signals of the genetic quality of the bearer. Because antlers are costly to produce (Ullrey 1983; Folstad et al. 1989), only individuals of high quality should be able to produce large antlers. It follows that individuals with large antlers should have the least stress-induced asymmetry (Møller 1993). A negative relationship between antler size and degree of asymmetry has been found in reindeer (*R. tarandus*; Markusson & Folstad

1997) and roe deer (*Capreolus capreolus*; Pelabon & van Breukelen 1998). In both cases, the authors suggested that asymmetry of antlers signaled male quality. In contrast, Solberg and Sæther (1993) did not find a negative relationship between asymmetry and antler size in moose (*Alces alces*), which may be an artifact of correlating number of antler points with degree of asymmetry. It is probable that a different index to antler size (e.g., antler length, spread, Boone and Crockett score; Nesbitt & Wright 1981) would be more appropriate in a species with a high degree of antler palmation such as moose.

Measures of relative asymmetry followed the pattern predicted by Møller (1993); measures of absolute asymmetry did not. As a character increases in size, its potential for absolute deviation from perfect bilateral symmetry also should increase. Baccus and Welch (1982) found that age (representative of antler size) and absolute asymmetry of antlers were correlated positively in sika deer (*Cervus nippon*). Similarly, we expected to observe increased absolute asymmetry as trait size increased in our population, but the relationship was poor. In contrast, relative asymmetry had a strong, negative relationship to size in antlers. Measures of relative asymmetry correct for differences in absolute size of a trait by expressing asymmetry as a percentage of trait size. Our observations are in agreement with those of Smith et al. (1982), who reported a negative relationship between measures of relative asymmetry and size in antlers of white-tailed deer. Unlike most secondary sexual traits that are geometrically simple and relatively uniform in size throughout life (feathers, combs, etc.), antlers in white-tailed deer are structurally complex and may be >9 times as large (Ditchkoff et al. 2000) in mature than immature deer. These characteristics suggest that relative asymmetry of antlers may be a more suitable measure of male quality than absolute asymmetry in white-tailed deer. For example, an overall 10-

cm difference between antlers of a highly ornamented mature deer can not be directly compared to a 10-cm difference in spikes of a young buck unless relative asymmetry is used. In actuality, 10 cm of variation between the highly complex antlers developed by a mature white-tailed deer may represent a greater capacity to cope with environmental stresses than 10 cm of variation between spikes of young male.

In contrast to the pattern of decreasing relative asymmetry with antler size, deer ≥ 6.5 years of age had a positive relationship between relative asymmetry and antler size. The handicap hypothesis of mate selection is based upon the premise that secondary sexual characters are costly to produce (Ullrey 1983; Folstad et al. 1989). Secondary sexual characters, through sexual selection, should increase in size to some threshold where benefits of the character are balanced by costs of production (Fisher 1930). Antlers in white-tailed deer ≥ 6.5 years of age may illustrate this threshold. Few structures in the animal kingdom possess a rate of tissue growth equal to that found in cervid antlers (Goss 1983), indicating that antlers may be among the most costly secondary sexual characters to produce from a nutritional perspective. Antlers of the magnitude possessed by deer ≥ 6.5 years of age may be approaching the upper threshold of production based upon nutrient requirements. Although relative asymmetry of antlers of deer ≥ 6.5 years of age was not greater than in other age classes, the positive relationship between asymmetry and antler size within this age class suggests that some of these deer may have experienced increased development of antlers at the expense of reduced symmetry. Nilsson (1994) found that asymmetry can be influenced by the rate at which nutrients are secured by an individual, and Baccus and Welch (1982) and Pelabon and van Breukelen (1998) noted elevated asymmetry in antlers of sika and roe deer, respectively, from high density

enclosures (e.g. nutritional stress). If antler size is indeed near its upper threshold in white-tailed deer ≥ 6.5 years of age, we would expect a positive relationship between asymmetry and antler size in this age category because of individuals who maximize antler development and experience greater nutritional stress and asymmetry.

Decreases in relative asymmetry with age can be explained through natural selection. Because asymmetry is a measure of quality of an individual, or its ability to cope with environmental stresses, we would expect that lower quality individuals (high asymmetry) would have greater probability of mortality throughout life (Møller 1997; Møller & Nielsen 1997). Because of elevated susceptibility to disease, parasitism, malnutrition, or predation, the proportion of low quality individuals should decrease in a cohort as it ages, creating a negative relationship between asymmetry and age. Our prediction that the degree of variability in asymmetry among individuals within a cohort should decrease as a cohort ages, also was supported in our population. It is common for populations of white-tailed deer to experience annual rates of mortality from natural causes that range from 25-30% (Gavin et al. 1984; Nelson & Mech 1986; DeYoung 1989). As a result, there is a propensity for natural selection to modify average quality of a cohort through time (Solberg & Sæther 1993). A negative relationship between age and asymmetry has been reported in sika deer (Baccus & Welch 1982), white-tailed deer (Smith et al. 1982), roe deer (Pelabon & van Breukelen 1998), and moose (Solberg & Sæther 1993). In contrast, Hayden et al. (1994) did not find this relationship in sika deer.

It would seem reasonable to hypothesize that if fluctuating asymmetry of antlers is a measure of quality in white-tailed deer, it should be correlated with actual measures of animal condition. For example, number of visible ribs has been correlated positively with

horn asymmetry in gemsbok (Møller et al. 1996). Body mass is a good measure of condition because it is ultimately the end result of how effective an animal has been at meeting its nutritional requirements, not only for growth, but for competing life-history demands. A strong negative relationship between body mass and relative asymmetry supports the hypothesis that asymmetry in antler morphology signals quality of an individual. Similarly, Solberg and Sæther (1993) reported a negative relationship between body size and asymmetry in moose.

The life history of white-tailed deer is characteristic of those members of Cervidae where display is an important function for antlers. Solitary cervids such as pudu (*Pudu puda*) and roe deer have maintained relatively primitive antlers that serve primarily as weapons for intrasexual combat (Putman 1988). In contrast, males of more social species (e.g., white-tailed deer, red deer, fallow deer, caribou) have evolved antlers that serve as both tools for ritualized combat and ornaments for signaling quality (Clutton-Brock 1982; Putman 1988). Evolution of intricate branching patterns and palmation in antlers of more social cervids is consistent with characteristics of a sexually selected trait. We posit that secondary sexual characters are an advertisement of quality, and the more complex and visibly stimulating they become, the better the signal as perceived by females of that species (Fisher 1930). However, little direct evidence exists to indicate that antlers are used as cues by female white-tailed deer during the breeding season. Furthermore, it has yet to be demonstrated that female white-tailed deer are capable of, or allowed by males to exercise, choice for mates during the breeding season. We did not incorporate any data on female deer into this study and so can only speculate on issues of female choice, but we did find that patterns of asymmetry among antlers are consistent with patterns predicted by

Møller (1993) of a trait that is selected for by females. These results suggest that further studies are needed to assess whether female choice is important in white-tailed deer during the breeding season and whether antlers are used as cues by females if it is found that females are selective.

Literature Cited

- Alexander, J. & Stimson, W. H. 1988 Sex hormones and the course of parasitic infection. *Parasitol. Today* **4**, 189-193.
- Andersson, M. 1982 Female choice selects for extreme length in a widowbird. *Nature* **299**, 818-820.
- Arcese, P. 1994 Harem size and horn symmetry in oribi. *Anim. Behav.* **48**, 1485-1488.
- Baccus, J. T. & Welch, R. D. 1982 Asymmetry in the antler structure of sika deer from the Edwards Plateau of Texas. In *Antler development in Cervidae*. (ed. R. D. Brown), pp. 211-221. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.
- Barnard, P. 1990 Male tail length, sexual display intensity and female sexual response in a parasitic African finch. *Anim. Behav.* **39**, 652-656.
- Bartos, L. & Hyanek, J. 1983a Social position in the red deer stag. I. The effect on developing antlers. In *Antler development in Cervidae*. (ed. R. D. Brown), pp. 451-462. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.
- Bartos, L. & Hyanek, J. 1983b Social position in the red deer stag. II. The relationship with developed antlers. In *Antler development in Cervidae*. (ed. R. D. Brown), pp. 436-466. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.

- Bergerud, A. T. 1973 Movement and rutting behavior of caribou (*Rangifer tarandus*) at Mount Albert, Quebec. *Can. Field Nat.* **87**, 357-369.
- Byers, J. A. 1997 *American pronghorn: social adaptations and the ghosts of predators past*. Chicago: Univ. Chicago Press.
- Clutton-Brock, T. H. 1982 The function of antlers. *Behaviour* **79**, 108-125.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer: behavior and ecology of two sexes*. Chicago: Univ. Chicago Press.
- Cook, R. L. 1984 Texas. In *White-tailed deer ecology and management* (ed. L. K. Halls), pp. 457-474. Harrisburg, PA: Stackpole Books.
- DeYoung, C. A. 1989 Mortality of adult male white-tailed deer in south Texas. *J. Wildl. Manage.* **53**, 513-518.
- Ditchkoff, S. S., Welch, E. R., Jr. & Lochmiller, R. L. 2000 Using cast antler characteristics to profile quality of white-tailed deer *Odocoileus virginianus* populations. *Wildl. Biol.* **6**, 23-28.
- Ditchkoff, S. S., Welch, E. R., Jr., Lochmiller, R. L., Masters, R. E., Dinkines, W. C. & Starry, W. R. 1996 Deer harvest characteristics during compound and traditional archery hunts. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* **50**, 391-396.
- Ditchkoff, S. S., Welch, E. R., Jr., Starry, W. R., Dinkines, W. C., Masters, R. E. & Lochmiller, R. L. 1997 Quality deer management at the McAlester Army Ammunition Plant: a unique approach. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* **51**, 389-399.

- Fisher, R. 1930 *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Folstad, I., Nilssen, A. C., Halvorsen, O. & Anderson, J. 1989 Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? *Oikos* **55**, 87-92.
- Gavin, T. A., Suring, L. H., Vohs, P. A., Jr. & Meslow, E. C. 1984 Population characteristics, spatial organization, and natural mortality in the Columbian white-tailed deer. *Wildl. Monogr.* **91**, 1-41.
- Geist, V. 1981 Behavior: adaptive strategies in mule deer. In *Mule and black-tailed deer of North America*. (ed. O. C. Wallmo), pp. 157-224. Lincoln, NE: University of Nebraska Press.
- Geist, V. 1991 Bones of contention revisited: did antlers enlarge with sexual selection as a consequence of neonatal security strategies? *Appl. Anim. Behav. Sci.* **29**, 453-469.
- Geist, V. 1998 *Deer of the world: their evolution, behavior, and ecology*. Mechanicsburg, PA: Stackpole Books.
- Goss, R. J. 1983 *Deer antlers, regeneration, evolution, and function*. New York: Academic Press.
- Gibson, R. M. & Guinness, F. E. 1980 Differential reproductive success in red deer stags. *J. Anim. Ecol.* **49**, 199-208.
- Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384-387.

- Hayden, T. J., Lynch, J. M. & O'Corry-Crowe, G. 1994 Antler growth and morphology in a feral sika deer (*Cervus nippon*) population in Killarney, Ireland. *J. Zool., Lond.* **232**, 21-35.
- Jacobson, H. A. & Reiner, R. J. 1989 Estimating age of white-tailed deer: tooth wear versus cementum annuli. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* **43**, 286-291.
- Leary, R. F. & Allendorf, F. W. 1989 Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends Ecol. Evol.* **4**, 214-217.
- Malyon, C. & Healy, S. 1994 Fluctuating asymmetry in antlers of fallow deer, *Dama dama*, indicates dominance. *Anim. Behav.* **48**, 248-250.
- Marchinton, R. L., Miller, K. V. & McDonald, J. S. 1995 Genetics. In *Quality whitetails: the why and how of quality deer management* (eds., K. V. Miller & R. L. Marchinton), pp. 169-189. Mechanicsburg, PA: Stackpole Books.
- Markusson, E. & Folstad, I. 1997 Reindeer antlers: visual indicators of individual quality? *Oecologia* **110**, 501-507.
- McDonald, D. 1989 Correlates of male mating success in a lekking bird with male-male cooperation. *Anim. Behav.* **37**, 1007-1022.
- Miller, K. V., Marchinton, R. L., Forand, K. J. & Johansen, K. L. 1987 Dominance, testosterone, and scraping activity in a captive herd of white-tailed deer. *J. Mamm.* **68**, 812-817.
- Min, S. E. 1997 Variation in sexually dimorphic traits of male pronghorns. *J. Mamm.* **78**, 31-47.

- Møller, A. P. 1988 Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* **332**, 640-642.
- Møller, A. P. 1990 Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**, 1185-1187.
- Møller, A. P. 1993 Patterns of fluctuating asymmetry in sexual ornaments predict female choice. *J. Evol. Biol.* **6**, 481-491.
- Møller, A. P. 1997 Developmental stability and fitness: a review. *Am. Nat.* **149**, 916-932.
- Møller, A. P., Cuervo, J. J., Soler, J. J. & Zamora-Munoz, C. 1996 Horn asymmetry and fitness in gemsbok, *Oryx g. gazella*. *Behav. Ecol.* **7**, 247-253.
- Møller, A. P. & Nielsen, J. T. 1997 Differential predation costs of a secondary sexual character: sparrowhawk predation in barn swallows. *Anim. Behav.* **54**, 1545-1551.
- Møller, A. P. & Thornhill, R. 1998 Bilateral symmetry and sexual selection: a meta-analysis. *Am. Nat.* **151**, 174-192.
- Morris, M. R. & Casey, K. 1998 Female swordtail fish prefer symmetrical sexual signals. *Anim. Behav.* **55**, 33-39.
- Nelson, M. E. & Mech, L. D. 1986 Mortality of white-tailed deer in northeastern Minnesota. *J. Wildl. Manage.* **50**, 691-698.
- Nesbitt W. H. & Wright, P. L. 1981 *Records of North American big game*. Alexandria, VA: Boone and Crockett Club.
- Nilsson, J. A. 1994 Energetic stress and the degree of fluctuating asymmetry: implications for a long-lasting honest signal. *Evol. Ecol.* **8**, 248-255.

- Palmer, A. R. & Strobeck, C. 1986 Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* **17**, 391-421.
- Pelabon, C. & van Breukelen, L. 1998 Asymmetry in antler size in roe deer (*Capreolus capreolus*): an index of individual and population conditions. *Oecologia* **116**, 1-8.
- Petrie, M., Halliday, T. R. & Sanders, C. 1990 Peahens prefer peacocks with elaborate trains. *Anim. Behav.* **41**, 323-331.
- Pruett-Jones, S. G. & Pruett-Jones, M. A. 1990 Sexual selection through female choice in Lawes' parotia, a lek-mating bird of paradise. *Evolution* **44**, 486-501.
- Putman, R. 1988 *The natural history of deer*. Ithaca, NY: Cornell University Press.
- SAS Institute Inc. 1990 *SAS/STAT user's guide*. Cary, NC: SAS Institute Inc..
- Severinghaus, C. W. 1949 Tooth development and wear as criteria for age in white-tailed deer. *J. Wildl. Manage.* **13**, 195-216.
- Smith, M. H., Chesser, R. K., Cothran, E. G. & Johns, P. E. 1982 Genetic variability and antler growth in a natural population of white-tailed deer. In *Antler development in Cervidae*. (ed. R. D. Brown), pp. 365-387. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.
- Solberg, E. J. & Sæther, B. E. 1993 Fluctuating asymmetry in the antlers of moose (*Alces alces*): does it signal male quality? *Proc. R. Soc. Lond. B* **254**, 251-255.
- Sullivan, M. S., Robertson, P. A. & Aebischer, N. A. 1993 Fluctuating asymmetry measurement. *Nature* **361**, 409-410.
- Swaddle, J. P. & Cuthill, I. C. 1994 Female zebra finches prefer males with symmetric chest plumage. *Proc. R. Soc. Lond. B* **258**, 267-271.

- Thornhill, R. 1992 Fluctuating asymmetry and the mating system of the Japanese scorpionfly, *Panorpa japonica*. *Anim. Behav.* **44**, 867-879.
- Thornhill, R. & Sauer, K. P. 1992 Genetic sire effects on the fighting ability of sons and daughters and mating success of sons in the scorpionfly (*Panorpa vulgaris*). *Anim. Behav.* **43**, 255-264.
- Townsend, T. W. & Bailey, E. D. 1981 Effects of age, sex, and weight on social rank in penned white-tailed deer. *Am. Mid. Nat.* **106**, 92-101.
- Ullrey, D. E. 1983 Nutrition and antler development in white-tailed deer. In *Antler development in Cervidae*. (ed. R. D. Brown), pp. 49-59. Kingsville, TX: Caesar Kleberg Wildlife Research Institute.
- Van Valen, L. 1962 A study of fluctuating asymmetry. *Evolution* **16**, 125-142.
- Wittzell, H. 1991 Directional selection on morphology in the pheasant, *Phasianus colchicus*. *Oikos* **61**, 394-400.
- Zahavi, A. 1975 Mate selection - a selection for a handicap. *J. Theor. Biol.* **53**, 205-214.
- Zuk, M., Thornhill, R. & Ligon, J. D. 1990 Parasites and mate choice in red jungle fowl. *Am. Zool.* **30**, 235-244.

Table 1. Correlation matrix reflecting relationships between measures of relative fluctuating asymmetry for antlers of white-tailed deer in southeastern Oklahoma, 1994-96.

Character		Score	Beam length	Basal circumference	Antler points
Score	<i>r</i>	1.000	-----	-----	-----
	<i>P</i>	0.000			
	<i>n</i>	213			
Beam length	<i>r</i>	0.231	1.000	-----	-----
	<i>P</i>	0.001	0.000		
	<i>n</i>	213	305		
Basal circumference	<i>r</i>	0.547	0.173	1.000	-----
	<i>P</i>	0.001	0.003	0.000	
	<i>n</i>	213	290	290	
Antler points	<i>r</i>	0.443	0.003	0.018	1.000
	<i>P</i>	0.001	0.958	0.761	0.000
	<i>n</i>	213	292	287	295

Figure 1. Age-specific changes in mean (\pm SE) measures of absolute and relative fluctuating asymmetry of antler score in white-tailed deer from a population in southeastern Oklahoma, 1994-1996. Means with different letters differ ($P \leq 0.05$) based upon Least Square Means analysis.

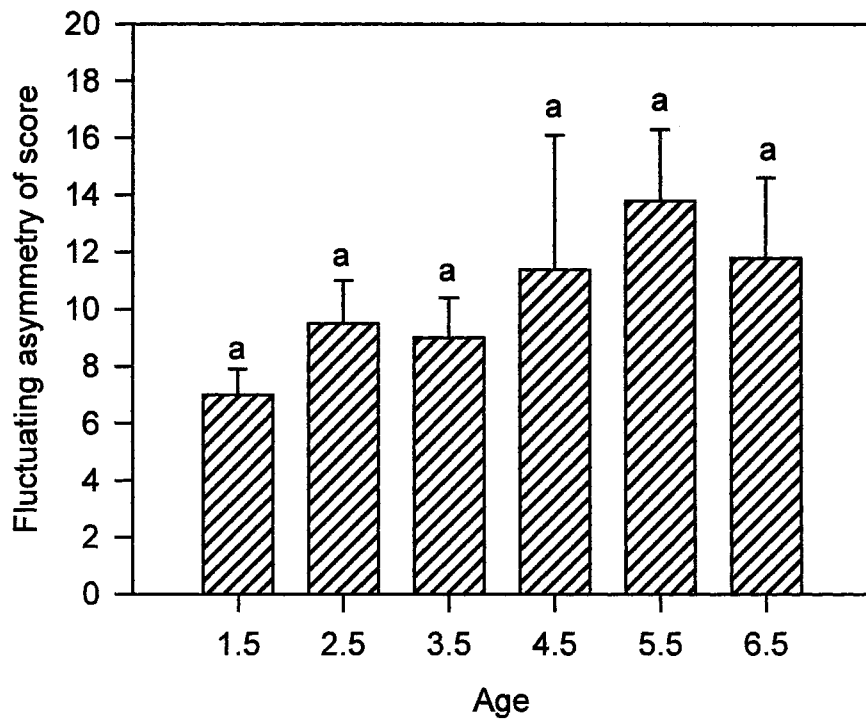
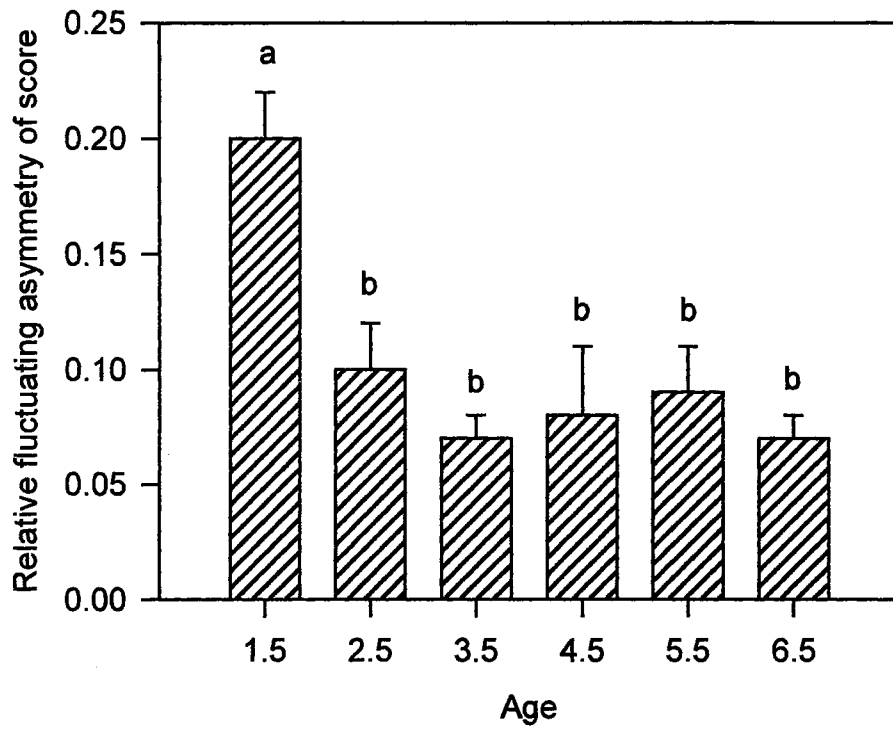


Figure 2. Simple linear regression depicting the relationship between age and relative asymmetry of antler score for white-tailed deer from a population in southeastern Oklahoma, 1994-1996 ($n = 214$).

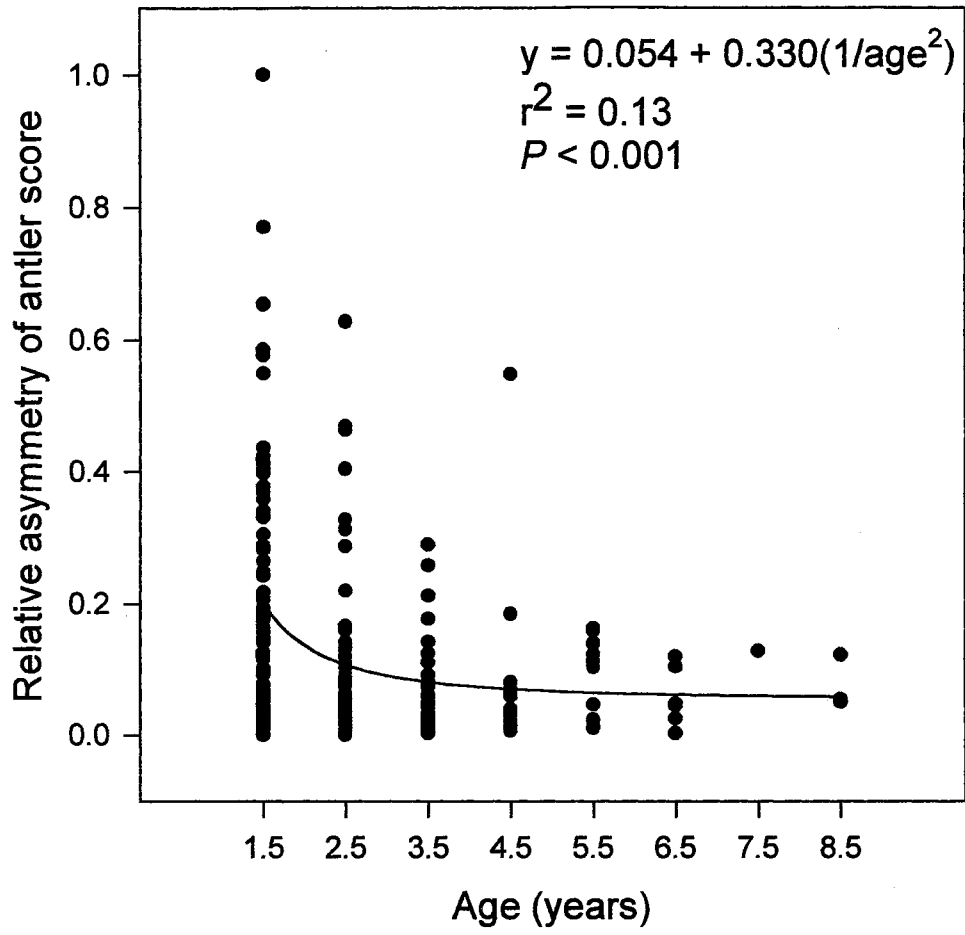


Figure 3. Simple linear regressions describing the relationships between score of the larger antler and Boone and Crockett score, and relative asymmetry of antler score for white-tailed deer from a population in southeastern Oklahoma, 1994-1996. Boone and Crockett score was calculated using the technique described by Nesbitt and Wright (1981).

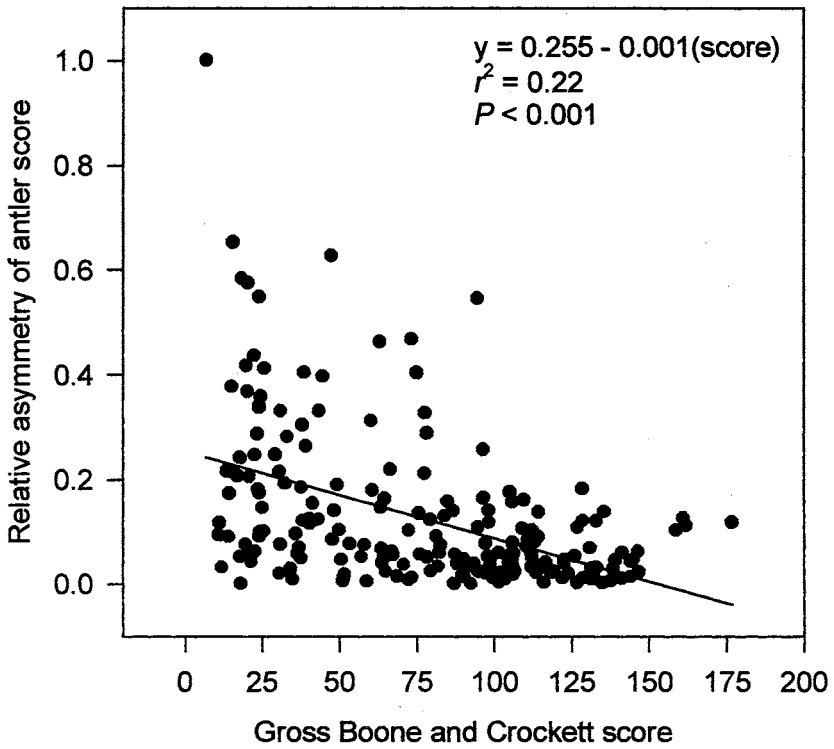
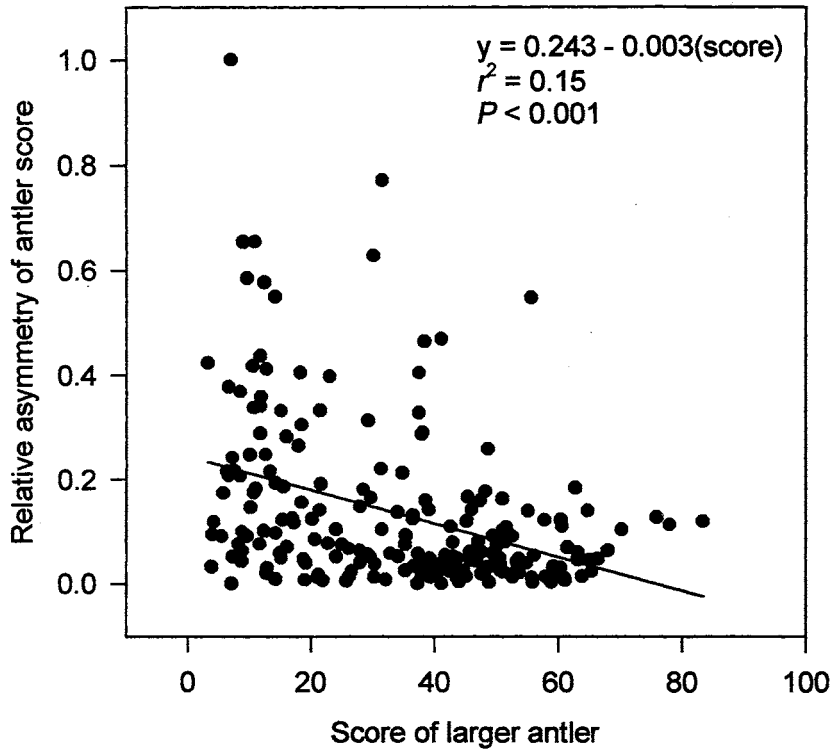


Figure 4. Regression relationships between Boone and Crockett score and relative fluctuating asymmetry of score by age class for white-tailed deer from a population in southeastern Oklahoma, 1994-1996. Boone and Crockett score was calculated using the technique described by Nesbitt and Wright (1981).

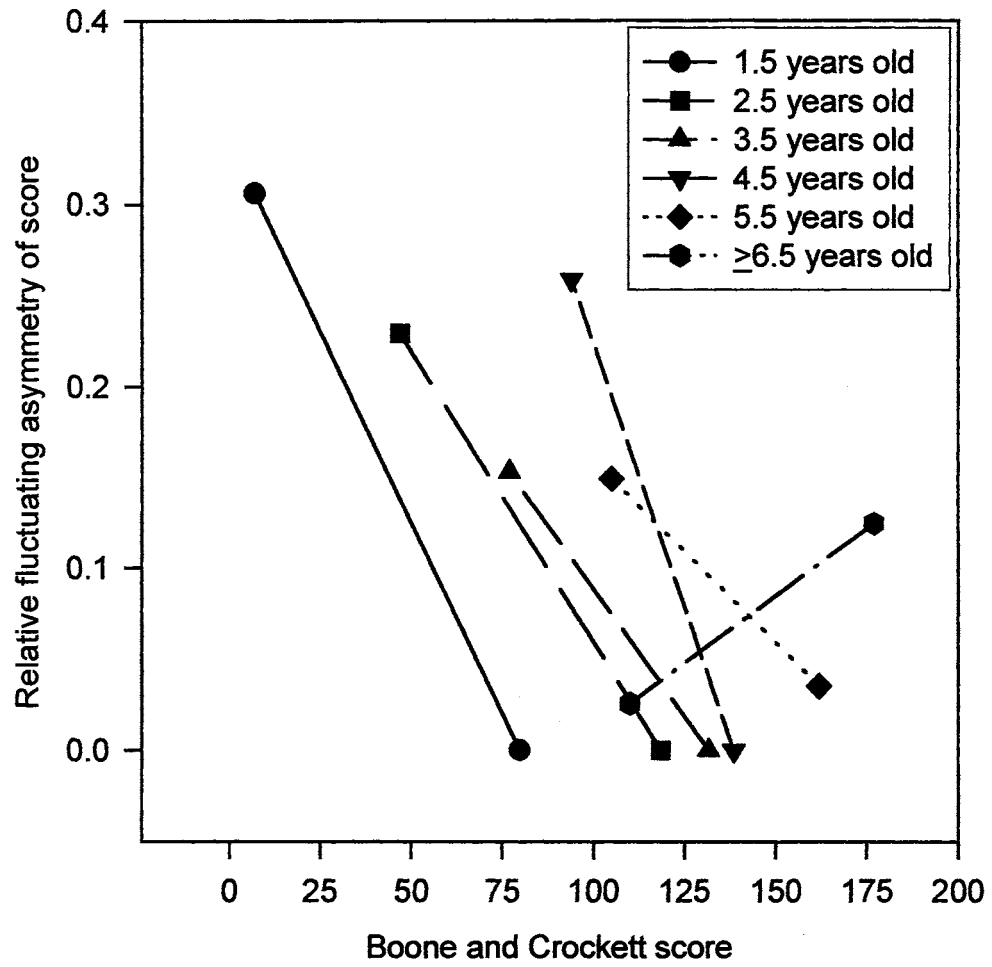


Figure 5. Correlative relationships between selected morphometric traits and relative asymmetry of antler score in white-tailed deer from a population in southeastern Oklahoma, 1994-1996.

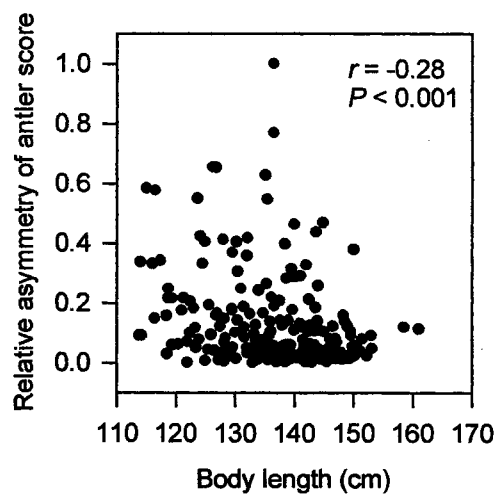
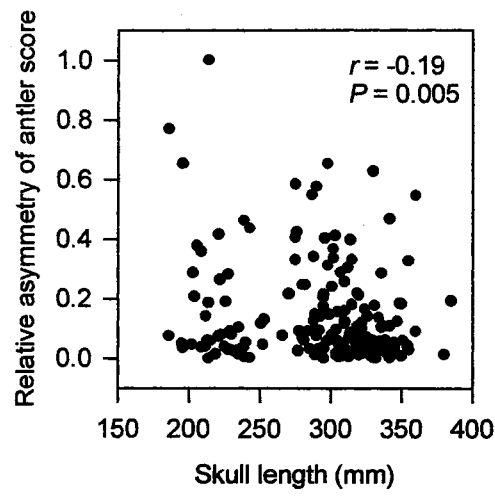
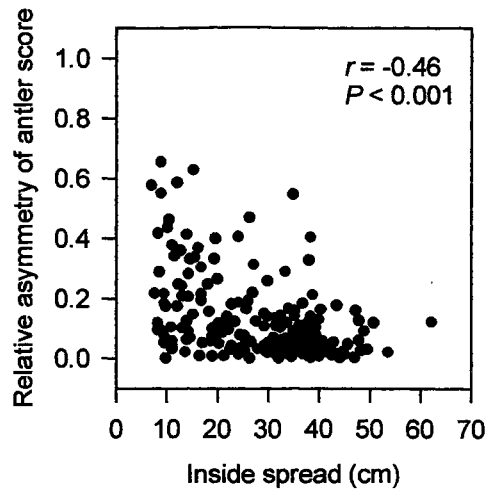
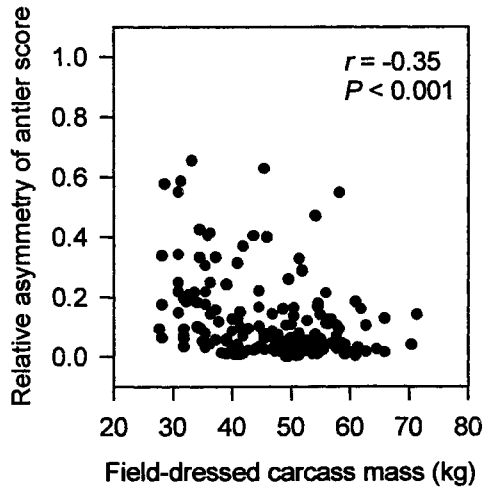
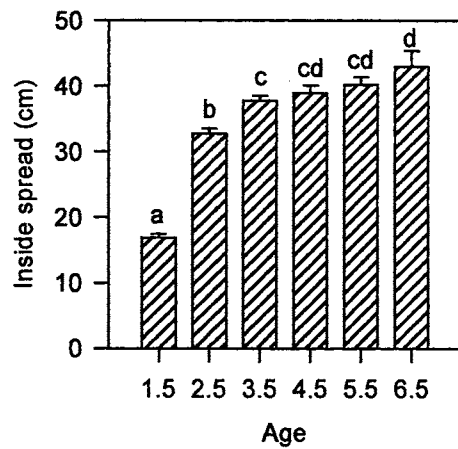
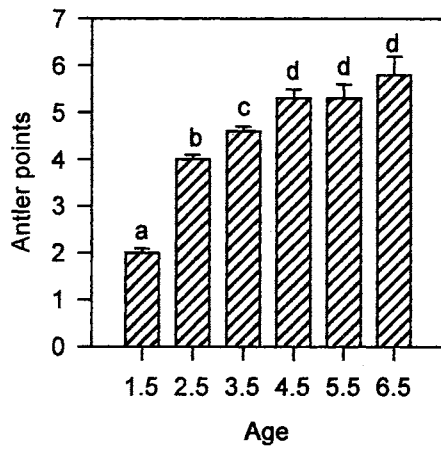
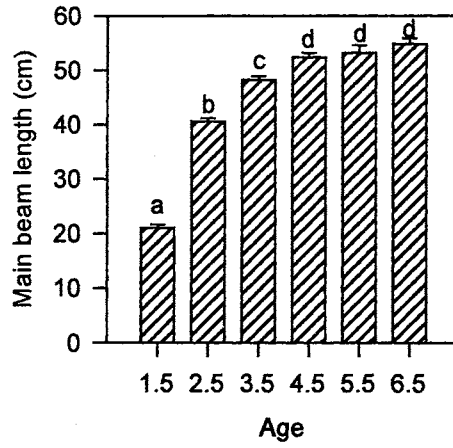
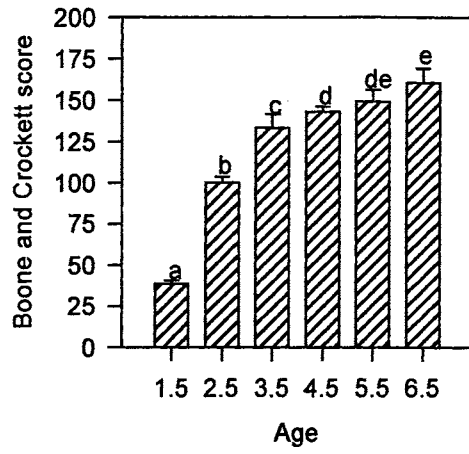
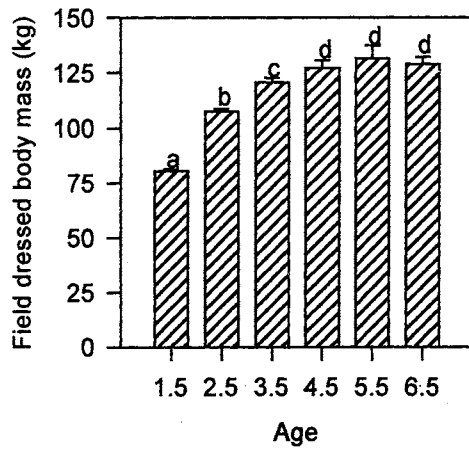


Figure 6. Age-specific differences in mean (\pm SE) body mass, Boone and Crockett score, main beam length, basal circumference, number of antler points, and inside spread of white-tailed deer from a population in southeastern Oklahoma, 1994-1996. Boone and Crockett score was calculated using the technique described by Nesbitt and Wright (1981). Means with different letters differ ($P \leq 0.05$) based upon Least Square Means analysis.



CHAPTER II

MHC-DRB EVOLUTION PROVIDES INSIGHT INTO PARASITE RESISTANCE IN WHITE-TAILED DEER

Summary

The major histocompatibility complex (MHC) is a gene complex that is closely linked to the vertebrate immune system due to its importance in antigen recognition and immune response to pathogens. As a result, the MHC has been considered the basis for genetic quality because of the devastating impact that parasites and disease can have on fitness. Yet our understanding of the MHC is incomplete, and most research to date has been conducted with humans and domestic livestock because of socio-economic factors. To improve our understanding of the MHC and parasite resistance in free-ranging species, we estimated infection levels of abomasal nematodes and ticks, and gathered genetic information on hunter-harvested white-tailed deer (*Odocoileus virginianus*) to determine whether the *DRB* region of the MHC contains alleles that are associated with abundance, intensity, and prevalence of these parasites. Mean abundance and intensity of *Haemonchus contortus* were strongly associated with phylogenetic groupings of *Odvi-DRB* alleles. Abundances and intensities of *Apteragia odocoilei*, *Ostertagia mossi*, and *O. dikmansii* were weakly associated with *Odvi-DRB* phylogenetic groupings. Infection of ectoparasitic ticks was strongly associated with *Odvi-DRB* alleles but had a positive

association with alleles from a different evolutionary lineage than abomasal nematodes. Our data suggest that allelic composition of the *Mhc-DRB* of white-tailed deer in southeastern Oklahoma may represent a genetic trade-off. Homozygosity between allelic lineages at *Mhc-DRB* provides strong resistance to 1 class of parasite, either abomasal nematodes or ectoparasitic ticks, but heterozygosity between allelic lineages may provide resistance to a greater number of pathogens.

Introduction

The major histocompatibility complex (MHC) is widely recognized as being closely linked to the vertebrate immune system due to its role in antigen recognition and immune response to pathogens (Klein 1986). Because of the MHC's potential effects on body condition and fitness, it has been examined in a wide array of species, including mammals (Trowsdale 1995), birds (Edwards and Potts 1996), fishes (Dixon et al. 1995), reptiles (Grossberger and Parham 1992), and amphibians (Radtkey et al. 1996). However, most of our knowledge of the MHC in free-ranging species has been limited to genetic organization, number of genes, and allelic diversity. In addition to functioning in immune response, several life-history traits appear to be influenced by genetic variation at MHC loci. For example, life span, mate selection, testicular volume, testosterone levels, egg and milk production, and spontaneous abortion have been associated with MHC-linked loci (Finch and Rose 1995; von Schantz et al. 1996). These observations have led others (Finch and Rose 1995) to refer to the MHC as a "life-history gene complex" that directly influences fitness, as has proposed in a model for its involvement in demography of animal populations (Lochmiller 1996).

The importance of the MHC to the life history of vertebrate species becomes apparent when examining the potential impact that parasites can have on fitness. Parasites can negatively influence fitness in vertebrate hosts by competing for resources (e.g., energy and nutrients), transmitting diseases that place further demands on the host, and causing secondary infection. Resources that would normally be used for maintenance, growth, or reproduction are lost or must be redirected to mount an immune response. Individuals that possess MHC characteristics enabling them to mount a rapid, effective response to parasitic assault may benefit from increased resources available for growth or reproduction (Lochmiller and Deerenberg 1999) and reduced risk of predation (Lochmiller 1996).

We have long recognized intraspecific variation in parasite resistance, and recently, relationships between allelic variation of the MHC and parasite-disease resistance have been documented (Blackwell 1996; Lessard et al. 1996; Outteridge 1996). Furthermore, evidence suggests that MHC heterozygosity influences fitness. These factors, because of their implications, have resulted in an abundance of MHC studies, and domestic ungulates have begun to receive considerable attention because of their economic importance. Work with Soay sheep (*Ovis aries*) has suggested that allelic variation of the MHC is associated with juvenile survival and resistance to intestinal nematodes (Paterson, Wilson & Pamberton 1998). Alleles that were associated with high parasite loads also were associated with low survivorship, suggesting that MHC-based resistance to parasites may be a good measure of individual quality. Similarly, in an effort to isolate alleles responsible for resistance to abomasal helminths, it was found that the ovine MHC was important in parasite resistance and certain alleles were associated with lower fecal egg

counts than other more common alleles (Schwaiger et al. 1995). Results from these studies suggest that resistance to intestinal helminths in ungulates may be associated with allelic variation at *Mhc-DRB*.

While our understanding of the MHC is improving with each new study, we are far from having a complete understanding of the function and importance of this gene complex. As a result, we investigated the role of the MHC in parasite resistance in a free-ranging population of white-tailed deer (*Odocoileus virginianus*) by estimating densities of abomasal nematodes and ectoparasitic ticks from hunter-harvested deer and determining allelic composition of the *Mhc-DRB* exon 2. We chose to study the *Mhc-DRB* because it is highly variable, is involved in immune defense, and has been the most widely studied MHC locus in Artiodactyla (Mikko and Andersson 1995; Swarbick et al. 1995; Mikko, Lewin & Andersson 1997; Van Den Bussche, Hooper & Lochmiller 1999).

Materials and Methods

We collected data from 150 adult, male deer that were harvested by hunters during October-November from 1995 to 1996 at the McAlester Army Ammunition Plant in southeastern Oklahoma, USA (34° 49' N, 95° 55' W). The 18,212-ha facility had been managed under objectives of quality deer management since 1989 (Ditchkoff et al. 1997). Density of deer on the area was about 12-13 deer/km². Vegetation was characterized by oak (*Quercus* spp.) uplands and bottoms interspersed with tallgrass prairie (*Andropogon virginicus*, *A. gerardii*, *Schizachyrium scoparium*) and brush communities (*Rhus* spp., *Ulmus alata*, *Prunus angustifolia*, *Diospyros virginiana*) in drainages and upland sites.

Immediately following harvest, deer were field-dressed and the abomasum removed, tied at both ends with string to avoid loss of contents, and frozen. Deer were aged by tooth wear and replacement (Severinghaus 1949). Abomasal contents were removed, diluted with water to 1,000 ml, and a 50-ml aliquot examined (Prestwood et al. 1973). Total nematodes in the abomasum were calculated by multiplying number of nematodes per 50-ml aliquot by 20. Nematodes were identified based upon structure of spicules and gubernacula (Kubat, Kocan & Davidson 1980). Ectoparasitic ticks (mainly *Amblyomma americanum* and *Ixodes scapularis*) were enumerated on the sternum of each deer prior to field-dressing using a 2.5- x 12.5-cm template (Sams et al. 1996). All ticks within the template were enumerated, and the count was used as an index of the degree of ectoparasite infestation.

We calculated abundance, intensity, and prevalence of each species of abomasal nematode (Margolis et al. 1982). Abundance was defined as mean number of abomasal nematodes per deer. We determined intensity of infection by calculating mean number of nematodes per deer that had >0 nematodes. Prevalence was the percentage of deer that had >0 nematodes. We calculated tick abundance but did not calculate intensity or prevalence of ticks because prevalence approached 100%.

Following harvest, approximately 1 g of liver tissue was collected and placed in lysis buffer, and DNA was isolated following standard protocols (Longmire, Maltbie & Baker 1997). We conducted polymerase chain reaction (PCR) amplification of *Mhc-DRB* exon 2 using primers LA31 and LA32 (Sigurdardottir et al. 1991). We identified allelic diversity of *Mhc-DRB* exon 2 using a modification of the single-stranded conformation

polymorphism (SSCP) analysis (Orita et al. 1989). A complete description of the genetic techniques have been reported previously (Van Den Bussche, Hooper & Lochmiller 1999).

Previous methods used to examine associations between parasites and the MHC in ungulates attempted to identify alleles that were associated with low parasite loads (Paterson, Wilson & Pamberton 1998; Schwaiger et al. 1995). Because little is known about the MHC in white-tailed deer and other cervids, we felt any attempt to associate specific alleles with parasite loads would be premature. Moreover, we detected 15 *Mhc-DRB* alleles in this population (Van Den Bussche, Hooper & Lochmiller 1999), which would limit our ability (e.g., statistical power) to detect associations between parasites and specific alleles. Therefore, we classified alleles into 1 of 2 allelic lineages (Table 1) based upon earlier phylogenetic analyses (Van Den Bussche, Hooper & Lochmiller 1999).

Evolution of the MHC typically occurs from point mutations rather than recombination, resulting in allelic lineages containing alleles that are likely similar from a functional standpoint because of amino acid sequences that are almost identical. Using the phylogenetic classification, we were then able to categorize the *Odvi-DRB* profiles of our deer into 3 groups. Deer with both *Odvi-DRB* alleles from lineage 1 were categorized as Type 11, and deer with both alleles from lineage 2 were categorized as Type 22. Deer with alleles from each of the two lineages were categorized as Type 12.

We compared parasite data between deer with different genetic characteristics (e.g., Types 11, 12, and 22) using generalized linear models (PROC GENMOD; SAS Institute, Inc. 1993) with a poisson distribution and log link. Generalized linear models are a broad class of statistics that allow analysis of data sets with a variety of distributions (Agresti 1996). Because generalized linear models do not assume normality or

homogeneity of variance like general linear models (e.g., ANOVA), we avoided inherent problems associated with transformations that do not satisfy all assumptions.

Results

We identified 6 different species of abomasal nematodes, *Haemonchus contortus* (25.8 ± 11.0 ; mean abundance \pm SE), *Apteragia odocoilei* (504.0 ± 35.0), *A. pursglovei* (3.3 ± 1.5), *Ostertagia dikmansi* (148.3 ± 16.7), *O. mossi* (58.4 ± 9.8), and *O. ostertagia* (3.0 ± 1.6), but *A. pursglovei*, and *O. ostertagia* were each found in ≤ 5 deer so statistical analyses on these species were not possible. Mean number of nematode species within the abomasum of each deer was 2.6. Mean abundance of abomasal nematodes in deer from our study area was 735.7 (SE = 52.7) nematodes/deer with abundance estimates ranging from 20 to 3,200.

Abundances of *H. contortus*, *O. mossi*, and *O. dikmansi* were greater among Type 22 deer than Types 11 or 12 deer (Table 2). However, Type 11 deer had greater abundance of *A. odocoilei*. Mean abundance of *H. contortus* was greater in 1.5 year-old deer with Type 22 *Odvi-DRB* characteristics (51.3 ± 30.7) than Type 11 (13.7 ± 9.3) or Type 12 (21.9 ± 12.3 ; Fig. 1a). We also found greater mean abundance of *H. contortus* in deer 2.5 and ≥ 3.5 years old with Type 22 genetic characteristics than Types 11 or 12. Mean abundance of *A. odocoilei* was greatest in Type 22 deer that were 1.5 (503.9 ± 66.9) and ≥ 3.5 years old (606.0 ± 99.2), but greatest in Type 11 deer (730.7 ± 215.2) that were 2.5 years old (Fig. 1b). Abundance of *O. mossi* followed patterns similar to *A. odocoilei* abundance, with 1.5 and ≥ 3.5 -year-old deer with Type 22 *Odvi-DRB* profiles having greater nematodes than Type 11 deer; Type 12 deer were intermediate (Fig. 1c).

Mean abundance of *O. dikmansii* was greater in Type 22, 1.5- (99.0 ± 23.9), 2.5- (75.4 ± 43.3), and ≥ 3.5 -year-old deer (77.5 ± 24.0) than Type 11 or 12 deer (Fig. 1d).

There were greater mean intensities of *H. contortus*, *O. mossii*, and *O. dikmansii* among Type 22 deer than Type 11 deer, but like abundance, intensity of *A. odocoilei* was greatest in Type 11 deer (Table 2). There were greater mean intensities of *H. contortus* for 1.5- (145.4 ± 76.1), 2.5- (417.6 ± 399.4), and ≥ 3.5 -year-old deer (42.6 ± 3.8) that had Type 22 *Odvi-DRB* profiles (Fig. 2a). *A. odocoilei* (Fig. 2b) infection intensities were greater in Type 22 deer that were 1.5 (503.9 ± 66.9) and ≥ 3.5 years old (605.9 ± 99.2) than Type 11 deer. Similarly, mean intensities of *O. mossii* were greater in Type 22 deer that were 1.5 (197.4 ± 29.0) and ≥ 3.5 years old (146.8 ± 43.9) than Type 11 deer. Mean intensities of *O. dikmansii* were greatest in 1.5- (140.2 ± 25.5) and 2.5-year-old deer (176.0 ± 88.5) that were Type 22, but greatest in Type 11 deer that were ≥ 3.5 years old (117.3 ± 33.0 ; Fig. 2d). In general, prevalence of infection with abomasal nematodes did not follow patterns of abundance or intensity (Fig. 3), however, we did find that prevalence of *O. dikmansii* was greater ($P = 0.017$) in Type 22 deer that were 1.5 years old than Type 11 deer.

Mean abundance of ectoparasitic ticks was greater in Type 11 (24.6 ± 4.9) than Type 22 deer (15.8 ± 2.7 ; Fig 4). Similarly, 2.5-year-old deer that were Type 11 (28.7 ± 12.6) had greater mean abundance of ticks than Type 22 deer (17.3 ± 5.1). Mean abundance of ticks between deer with *Odvi-DRB* Types 11 and 22 were similar for 1.5- and ≥ 3.5 -year-old deer. Mean tick abundance was greatest in Type 12 deer ≥ 3.5 years of age (39.4 ± 7.1), but least among deer 1.5 years old (8.3 ± 3.6).

Discussion

We detected a significant relationship between abundance and intensity of abomasal nematodes, and allelic composition at *Odvi-DRB* exon 2. Individuals with both alleles from allelic lineage 1 (Type 11) had lower infection levels of *H. contortus* than Type 22 deer, while Type 12 deer had intermediate levels of infection. Similar trends were found with *A. odocoilei*, *O. mossi*, and *O. dikmansi*. These data suggest that alleles of *Odvi-DRB* are codominant, a common trait among MHC loci. Codominant alleles in the MHC could theoretically double the number of pathogens that a host could mount an immune response against. Because of codominance, heterozygosity at MHC loci could increase recognition of and response to foreign pathogens, thereby decreasing susceptibility to disease, and potentially increasing lifetime fitness (Apanius et al. 1997). Similar relationships were found when examining associations between resistance of sheep to intestinal nematodes and characteristics of the *Mhc-DRB* (Paterson, Wilson & Pamberton 1998). They noted that some *Mhc-DRB* characteristics, through suppression of parasite infestations, can lead to increased probability of survival.

Because *H. contortus* is probably the most pathogenic abomasal nematode of white-tailed deer in North America (Prestwood and Kellogg 1971; Prestwood et al. 1973), we expect that selection pressures on the MHC by this species would be greater than pressures exerted by less pathogenic species such as *A. odocoilei*, *O. mossi*, and *O. dikmansi*. Severe infection with *H. contortus* can result in lesions, blood loss, and sometimes death (Prestwood and Pursglove 1981); however, we did not encounter severe infestations in our study. *Apteragia odocoilei*, *O. mossi*, and *O. dikmansi*, while very

common in deer, rarely promote clinical symptoms or serious debilitation in their host (Prestwood and Pursglove 1981). Although not as strong, we detected similar relationships between these parasitic species and *Odvi-DRB*. These results suggest that either different alleles in the same evolutionary lineage are associated with these abomasal nematodes, or the same alleles can respond to all 4 species of nematode. Activation of immune response to suppress *H. contortus* infections has been shown previously to suppress other species of intestinal strongyles (Stewart 1953, 1955).

While alleles from lineage 1 of *Odvi-DRB* appeared to negatively influence levels of infection with abomasal nematodes, these same alleles were associated positively with tick abundance. Ticks are the most important ectoparasite of deer in North America and are found across most of their range (Strickland, Gerrish & Smith 1981). Although not usually associated with mortality in adult deer, their impact on neonates can at times indirectly increase risk of mortality (Bolte, Hair & Fletcher 1970; Logan 1992; Sams et al. 1996). Severe infestations may induce blood loss, secondary infection, and disease transmission and can result in anemia, weight loss, or death (Stewart 1955; Strickland, Gerrish & Smith 1976). Our understanding of the MHC and its functionality (e.g., peptide binding characteristics) suggests that parasites as different as abomasal nematodes and ticks would be associated with, at the very least, different alleles. It is not surprising that these parasites were associated with different allelic lineages.

The discovery that abomasal nematodes and ticks are associated with alleles from different clades at *Odvi-DRB* suggests that immune tradeoff may occur with regard to allelic composition at this locus. Both abomasal nematodes and ticks are prevalent parasites in Oklahoma deer (Sams et al. 1996, 1998) and at times can adversely affect deer

populations, as described earlier. Considerable diversity has been documented between allelic lineages of *Odvi-DRB* (Van Den Bussche, Hooper & Lochmiller 1999), suggesting that MHC evolution in these deer is driven by the need for immune defenses for multiple pathogens. As a result, it may be advantageous for deer that are heterozygous for clades of *Odvi-DRB* alleles because of resistance to more pathogens. Ultimately, decreased parasitism due to this form of heterozygosity (between clades) could lead to greater fitness through increased attractiveness to mates, social status, resource acquisition, and survival (Prestwood and Pursglove 1981; Borgia and Collis 1989).

While these data suggest that *Odvi-DRB* is linked to infection levels of abomasal nematodes and ticks in white-tailed deer, it does not imply that other portions of the MHC are not involved with antigen recognition and immune response to these classes of parasites. Our investigation was limited to a subset ($n = 15$) of alleles at 1 locus of the MHC. Recent work has resulted in the discovery of 3 new *Odvi-DRB* alleles in white-tailed deer (Ross 1999), and considering the high variability of the vertebrate MHC (Edwards and Potts 1996), this study has only begun mapping the MHC in Artiodactyla. Further research should be aimed at detecting relationships between the MHC and pathogens and investigating the effect that specific alleles have on the fitness, survival, and evolution of their host.

References

- Apanius, V., Penn, D., Slev, P. R., Ruff, L. R. & Potts, W. K. (1997) The nature of selection on the major histocompatibility complex. *Critical Reviews in Immunology*, **17**, 179-224.

- Bartos, L., Rezac, P., Siler, J., Buricova, M. & Ziegrosser, P. (1992) Social status and parasitic infection in red deer stags. *The biology of deer* (ed. R. D. Brown), p. 149. Springer-Verlag, New York, New York.
- Blackwell, J. M. (1996) Genetic susceptibility to Leishmanial infections: studies in mice and man. *Parasitology* **112**, s67-s74.
- Bolte, J. R., Hair, J. A. & Fletcher, J. (1970) White-tailed deer mortality following tissue destruction induced by lone star ticks. *The Journal of Wildlife Management*, **34**, 546-552.
- Borgia, G. & Collis, K. (1989) Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. *Behavioral Ecology and Sociobiology*, **25**, 445-454.
- Ditchkoff, S. S., Welch, E. R., Jr., Lochmiller, R. L., Masters, R. E., Dinkines, W. C. & Starry, W. R. (1996) Deer harvest characteristics during compound and traditional archery hunts. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, **50**, 391-396.
- Ditchkoff, S. S., Welch, E. R., Jr., Starry, W. R., Dinkines, W. C., Masters, R. E. & Lochmiller, R. L. (1997) Quality deer management at the McAlester Army Ammunition Plant: a unique approach. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, **51**, 389-399.
- Dixon, B., Van Erp, S. H. M., Rodrigues, P. N. S., Egberts, E. & Stet R. J. M. (1995) Fish major histocompatibility complex genes: an expansion. *Developmental and Comparative Immunology*, **19**, 109-133.

- Edwards, S. V. & Potts, W. K. (1996) Polymorphisms of genes in the major histocompatibility complex: implications for conservation genetics of vertebrates. *Molecular genetic approaches in conservation* (eds. T. B. Smith & R. K. Wayne), pp. 214-237. Oxford University Press, Oxford, England.
- Eve, J. H. & Kellogg, F. E. (1977) Management implications of abomasal parasites in southeastern white-tailed deer. *The Journal of Wildlife Management*, **41**, 169-176.
- Finch, C. E. & Rose, M. R. (1995) Hormones and the physiological architecture of life history evolution. *Quarterly Review of Biology*, **70**:1-52.
- Grossberger, D. & Parham, P. (1992) Reptilian class I major histocompatibility complex genes reveal conserved elements in class I structure. *Immunogenetics*, **36**, 166-174.
- Klein, J. (1986) *Natural history of the major histocompatibility complex*. John Wiley and Sons, New York, New York.
- Kubat, G., Kocan, A. A. & Davidson, W. R. (1980) *Identification of abomasal parasites of white-tailed deer*. Wildlife Disease Association, Ames, Iowa.
- Lessard, M., Hutchings, D. L., Spencer, J. L., Lillehoj, H. S. & Gavora, J. S. (1996) Influence of Mareks-disease virus-strain AC-1 on cellular immunity in birds carrying endogenous viral genes. *Avian Diseases*, **40**:645-653.
- Lochmiller, R. L. (1996) Immunocompetence and animal population regulation. *Oikos*, **76**, 594-602.
- Lochmiller, R. L. & Deerenberg, C. (1999) Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*. In press.

- Logan, T. (1992) Study of white-tailed deer fawn mortality on Cookson Hills Deer Refuge, eastern Oklahoma. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Game Commissioners*, **25**:27-39.
- Longmire, J. L., Maltbie, M. & Baker, R. J. (1997) Use of "lysis buffer" in DNA isolation and its implications for museum collections. *Occasional Papers, The Museum, Texas Tech University, Lubbock*, **163**, 1-3.
- Margolis, L., Esch, G. W., Holmes, J. C., Kuris, A. M. & Schad, G. A. (1982) The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology*, **68**, 131-133.
- Mikko, S. & Andersson, L. (1995) Low major histocompatibility complex class II diversity in European and North American moose. *Proceedings of the National Academy of Science USA*, **92**, 4259-4263.
- Mikko, S., Lewin, H. A. & Andersson, L. (1997) A phylogenetic analysis of cattle *DRB3* alleles with a deletion of codon 65. *Immunogenetics* **47**, 23-29.
- Orita, M., Iwahana, H., Kanazawa, H., Hayashi, K. & Sekiya, T. (1989) Detection of polymorphisms of human DNA by gel electrophoresis as single-stranded conformation polymorphisms. *Proceedings of the National Academy of Science USA*, **86**, 2766-2770.
- Outteridge, P. M., Andersson, L., Douch, P. G. C., Green, R. S., Gwakisa, P. S., Hohenhaus, M. A. & Mikko, S. (1996) The PCR typing of MHC-DRB genes in the sheep using primers for an intronic microsatellite: application to nematode parasite resistance. *Immunology and Cell Biology*, **74**, 330-336.

- Paterson, S., Wilson, K. & Pamberton, J. M. (1998) Major histocompatibility complex variation associated with juvenile survival and parasite resistance in a large unmanaged ungulate population (*Ovis aries L.*). *Proceedings of the National Academy of Science USA*, **95**, 3714-3719.
- Prestwood, A. K., Hayes, F. A., Eve, J. H. & Smith, J. F. (1973) Abomasal helminths of white-tailed deer in southeastern United States, Texas, and the Virgin Islands. *Journal of the American Veterinary Medical Association*, **163**, 556-561.
- Prestwood, A. K. & Kellogg, F. E. (1971) Naturally occurring Haemonchosis in a white-tailed deer. *Journal of Wildlife Diseases*, **7**, 133-134.
- Prestwood, A. K. & Pursglove, S. R., Jr. (1981) Gastrointestinal nematodes. *Diseases and parasites of white-tailed deer* (eds. W. R. Davidson, F. A. Hayes, V. F. Nettles & F. E. Kellogg), pp. 318-350. Tall Timbers Research Station, Tallahassee, Florida.
- Radtkey, R. R., Becker, B., Miller, R. D., Riblet, R. & Case, T. J. (1996) Variation and evolution of class I Mhc in sexual and parthenogenetic geckos. *Proceedings of the Royal Society of London, B*, **263**, 1023-1032.
- Ross, T. G. (1999) Genetic variation and population differentiation in white-tailed deer (*Odocoileus virginianus*) revealed by PCR-SSCP of the major histocompatibility complex. M.S. thesis, Oklahoma State University, Stillwater, Oklahoma.
- Sams, M. G., Lochmiller, R. L., Qualls, C. W., Jr., Leslie, D. M., Jr. & Payton, M. E. (1996) Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. *Journal of Mammalogy*, **77**, 179-190.

- Sams, M. G., Lochmiller, R. L., Qualls, C. W., Jr. & Leslie, D. M., Jr. (1998) Sensitivity of condition indices to changing density in a white-tailed deer population. *Journal of Wildlife Diseases*, **34**, 110-125.
- SAS Institute, Inc. (1993) *SAS/STAT software: the genmod procedure*. Release 6.09. SAS Institute, Inc., Cary, North Carolina. Technical Report P-243.
- Schwaiger, F. -W., Gostomski, D., Stear, M. J., Duncan, J. L., McKellar, Q. A., Epplen, J. T. & Buitkamp, J. (1995) An ovine major histocompatibility complex *DRB1* allele is associated with low faecal egg counts following natural, predominantly *Ostertagia circumcincta* infection. *International Journal of Parasitology*, **25**, 815-822.
- Severinghaus, C. W. (1949) Tooth development and wear as criteria for age in white-tailed deer. *The Journal of Wildlife Management*, **13**:195-216.
- Sigurdardottir, S., Borsch, C., Gustaffson, K. & Andersson, L. (1991) Cloning and sequence analysis of 14 DRB alleles of the bovine major histocompatibility complex by using the polymerase chain reaction. *Animal Genetics*, **22**, 199-209.
- Stewart, D. F. (1953) Studies on resistance of sheep to infestation with *Haemonchus contortus* and *Trichostrongylus* spp. and on the immunological reactions of sheep exposed to infestation. V. The nature of the 'self-cure' phenomenon. *Australian Journal of Agricultural Research*, **4**, 100-117.
- Stewart, D. F. (1955) 'Self-cure' in nematode infestations in sheep. *Nature (London)*, **176**, 1273-1274.
- Strickland, R. K., Gerrish, R. R., Hourrigan, J. L. & Schubert, G. O. (1976) *USDA, Animal and Plant Health Inspection Service Agricultural Handbook No. 485*.

- Strickland, R. K., Gerrish, R. R. & Smith, J. S. (1981) Arthropods. *Diseases and parasites of white-tailed deer* (eds. W. R. Davidson, F. A. Hayes, V. F. Nettles & F. E. Kellogg), pp. 363-389. Tall Timbers Research Station, Tallahassee, Florida.
- Swarbick, P. A., Schwaiger, F-W., Epplen, J. T., Buchan, G. S., Griffin, J. F. T. & Crawford, A. M. (1995) Cloning and sequencing of expressed *DRB* genes of the red deer (*Cervus elaphus*) Mhc. *Immunogenetics*, **42**, 1-9.
- Trowsdale, J. (1995) "Both bird and man and beast:" comparative organization of the MHC genes. *Immunogenetics*, **41**, 1-17.
- Van Den Bussche, R. A., Hooper, S. R. & Lochmiller, R. L. (1999) Characterization of *Mhc-DRB* allelic diversity in white-tailed deer (*Odocoileus virginianus*) provides insight into *Mhc-DRB* allelic evolution in Cervidae. *Immunogenetics*, **49**, 429-437.
- von Schantz, T., Wittzell, H., Goransson, G., Grahn, M. & Persson, K. (1996) MHC genotype and male ornamentation: evidence for the Hamilton-Zuk model. *Proceedings of the Royal Society of London, B*, **263**, 265-271.

Table 1. Categorization of alleles of the *Mhc-DRB* (*Odvi*) exon 2 found in white-tailed deer from southeastern Oklahoma, USA, into evolutionary lineages based upon phylogenetic analysis^a.

Allelic lineage 1	Frequency (%)	Allelic lineage 2	Frequency (%)
<i>Odvi-DRB*01</i>	3.9	<i>Odvi-DRB*02</i>	0.8
<i>Odvi-DRB*03</i>	3.9	<i>Odvi-DRB*05</i>	57.0
<i>Odvi-DRB*04</i>	42.2	<i>Odvi-DRB*06</i>	1.6
<i>Odvi-DRB*09</i>	1.6	<i>Odvi-DRB*07</i>	28.1
<i>Odvi-DRB*13</i>	1.6	<i>Odvi-DRB*08</i>	2.3
<i>Odvi-DRB*14</i>	14.1	<i>Odvi-DRB*10</i>	3.1
<i>Odvi-DRB*15</i>	0.8	<i>Odvi-DRB*11</i>	10.9
		<i>Odvi-DRB*12</i>	8.6

^a Evolutionary groupings were based upon phylogenetic analysis of Van Den Bussche et al. (1999).

Table 2. Mean abundance, mean intensity, and prevalence of abomasal parasites of adult, male white-tailed deer from a population in southeastern Oklahoma, USA with different characteristics of the *Odvi-DRB* exon 2.

Parasite	Mean abundance						Mean intensity						Prevalence ^a					
	<i>Odvi-DRB</i> 11		<i>Odvi-DRB</i> 12		<i>Odvi-DRB</i> 22		<i>Odvi-DRB</i> 11		<i>Odvi-DRB</i> 12		<i>Odvi-DRB</i> 22		<i>Odvi-DRB</i>					
	(n = 20)		(n = 31)		(n = 38)													
	Mean	SE	Mean	SE	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	11	12	22
<i>H. contortus</i>	5.7 a ^b	3.3	12.4 b	5.0	47.2 c	25.1	3	38.2 a	8.1	6	64.2 b	10.0	10	179.3 c	85.0	0.15	0.19	0.26
<i>A. odocoilei</i>	560.9 a	82.8	440.4 b	46.3	526.0 c	58.3	20	560.9 a	82.8	31	440.4 b	46.3	38	526.0 c	58.3	1.00	1.00	1.00
<i>O. mossi</i>	141.8 a	50.8	128.2 b	19.0	168.2 c	24.4	17	166.8 a	58.9	24	165.6 a	18.4	31	206.2 b	25.3	0.85	0.77	0.82
<i>O. dikmansi</i>	33.8 a	13.7	40.1 b	10.2	86.3 c	19.3	7	96.5 a	26.5	15	83.0 b	14.3	24	136.7 c	25.5	0.35	0.48	0.63
Total	745.0 a	117.3	609.4 b	59.6	844.7 c	94.4	20	745.0 a	117.3	31	609.4 b	59.6	38	844.7 c	94.4	1.00	1.00	1.00

^a Sample sizes (*n*) for prevalence estimates are the same as for mean abundance estimates.

^b Means in the same row and category (e.g., abundance or intensity) with different letters are different ($P < 0.05$).

Figure 1. Mean abundance (\pm SE) of 4 species of abomasal nematodes in adult, male white-tailed deer from Oklahoma. Deer were separated based upon age and allelic profile of the *Odvi-DRB*. Means with different letters within an age class are different ($P < 0.05$) based upon analyses using generalized linear models.

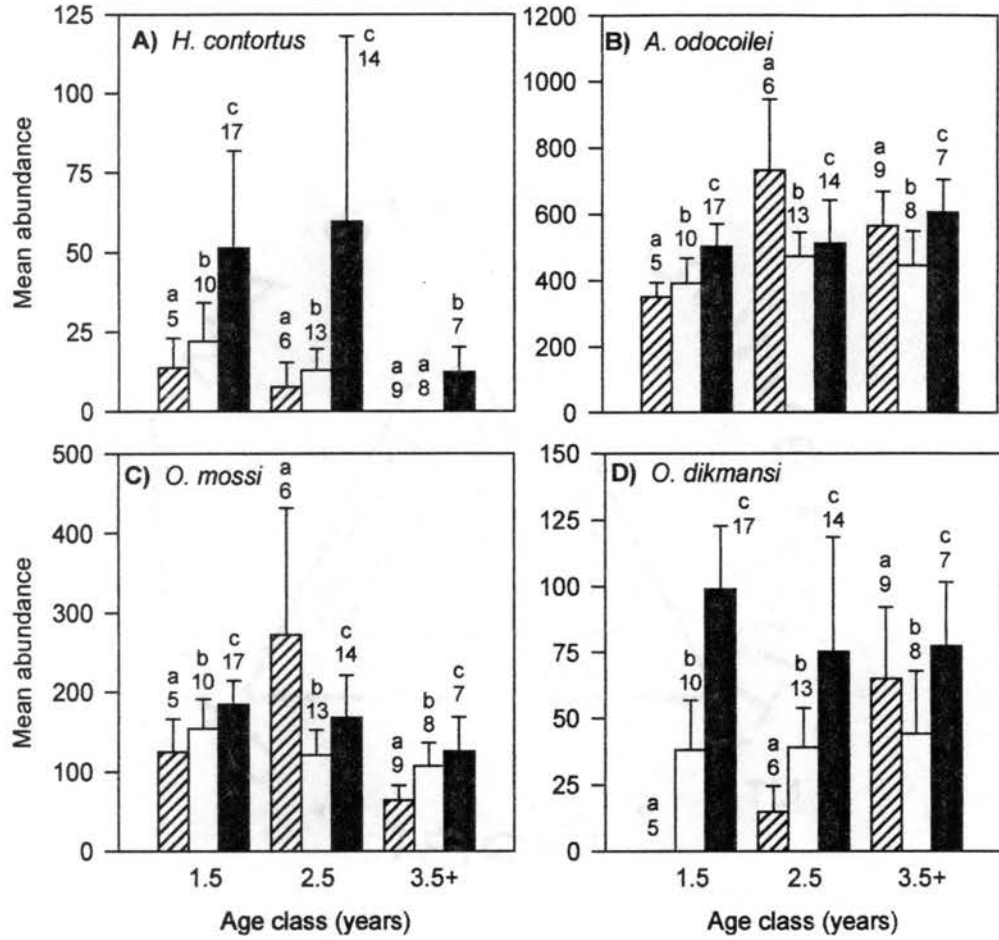
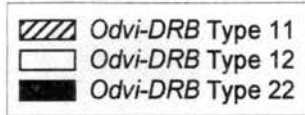


Figure 2. Mean intensity (\pm SE) of 4 species of abomasal nematodes in adult, male white-tailed deer from Oklahoma. Deer were separated based upon age and allelic profile of the *Odvi-DRB*. Means with different letters within an age class are different ($P < 0.05$) based upon analyses using generalized linear models.

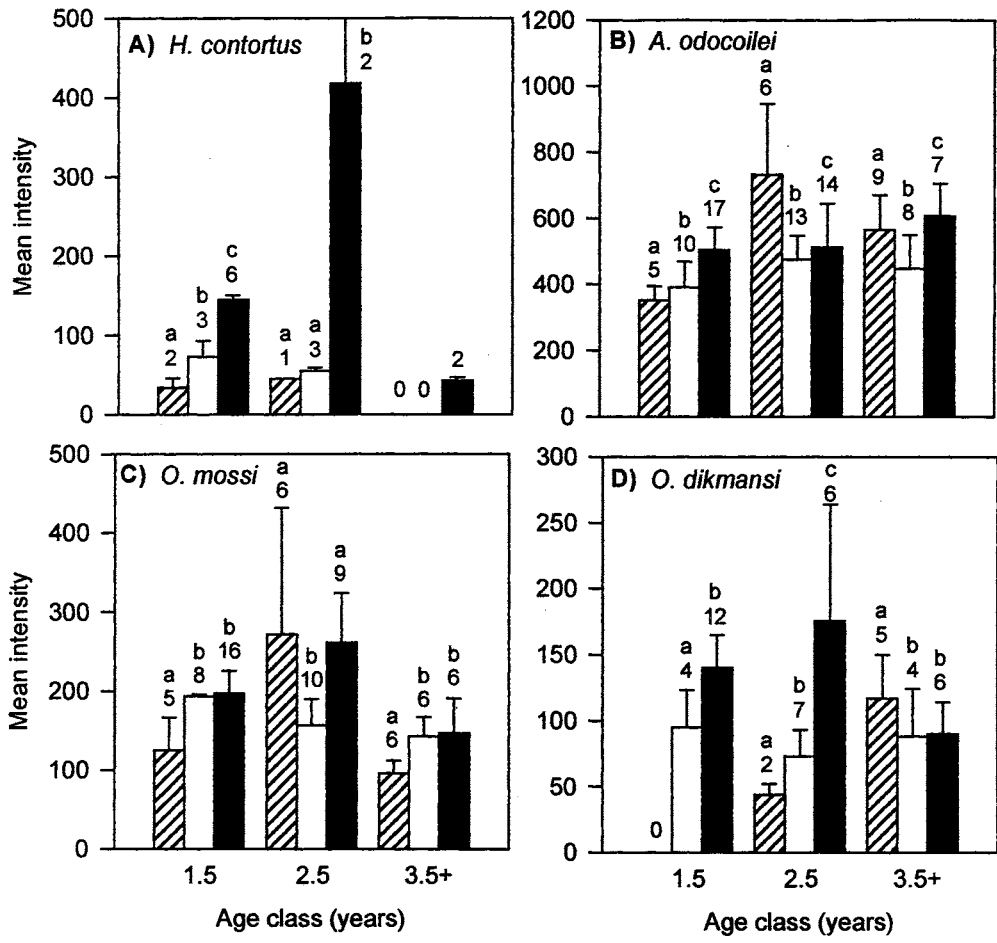
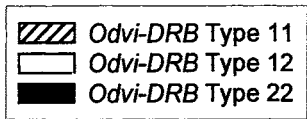


Figure 3. Prevalence of 4 species of abomasal nematodes in adult, male white-tailed deer from Oklahoma. Deer were separated based upon age and allelic profile of the *Odvi-DRB*. Means within an age class that are labeled with an (*) are different based upon analyses using generalized linear models.

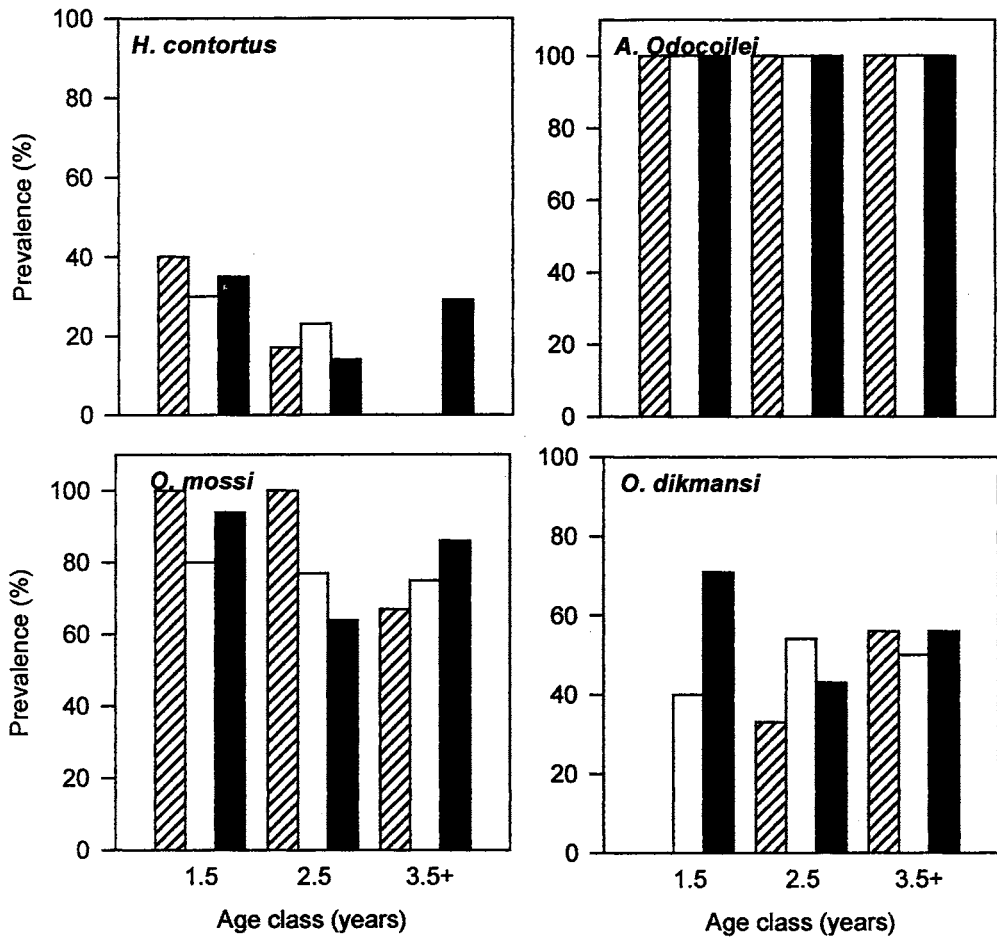
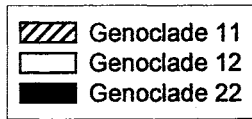
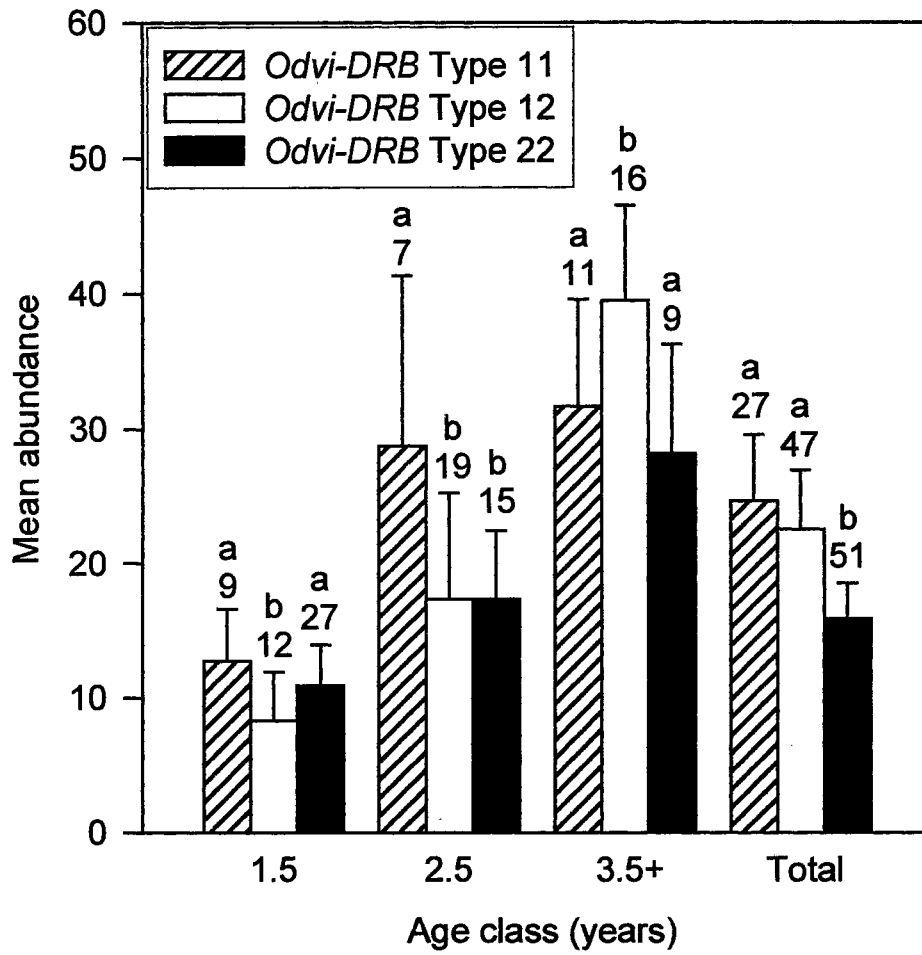


Figure 4. Mean abundance (\pm SE) of ticks on the sternum of adult, male white-tailed deer from Oklahoma. Deer were separated based upon age and allelic profile of the *Odvi-DRB*.



CHAPTER III

MHC-ASSOCIATED VARIATION IN SECONDARY SEXUAL TRAITS OF WHITE-TAILED DEER: EVIDENCE FOR “GOOD GENES” ADVERTISEMENT

Summary

“Good genes” hypotheses of mate selection predict that development of a secondary sexual character can be an honest advertisement of heritable male quality. We explored this hypothesis using a cervid model (adult, male white-tailed deer; *Odocoileus virginianus*) to determine whether antler development provides honest signals to potential mates of a male’s genetic quality. We compared antler, morphometric, hormonal, and parasitic data collected from hunter-harvested deer to characteristics of the *Mhc-DRB* (*Odvi*), the most widely studied gene of the major histocompatibility complex in Artiodactyla. We detected positive associations between *Odvi-DRB* heterozygosity and antler development and body mass, suggesting that antler development and body mass may be associated with pathogen resistance in deer and hence may be an honest signal of genetic quality. Individuals that were heterozygous at *Odvi-DRB* had greater levels of serum testosterone during the breeding season, possibly because those individuals were better able to cope with stresses related to breeding activity. Although we failed to detect relationships between genetic characteristics at the MHC and magnitude of parasitic infections, we did observe a negative relationship between degree of antler development

and overall abundance of abomasal helminths within a host. Our observations provide support for the hypothesis that antler development in cervids such as white-tailed deer is an honest signal of genetic quality. These are the first data to identify an association between antler development and signals of heritable fitness in Cervidae.

Introduction

Hamilton and Zuk (1982) have argued that female mate preference in polygamous species is closely linked to parasitism and their potential mate's exhibited resistance. Increased resistance to parasitism would be provided to offspring if a mate was chosen that had exceptional resistance to parasites based on genetic quality. Folstad and Karter (1992) expanded upon this theory, stating that males display their resistance through increased development of ornamentation and secondary sexual characters. Increased ornamentation, such as plumes, bright coloration, and antlers, is driven by elevated levels of testosterone and other hormones (Silverin 1980, Adkins-Regan 1981, Morris and Bubenik 1982). However, elevated levels of some hormones may reduce immunocompetence either directly (e.g., immunosuppressive steroids; Grossman 1984, Alexander and Stimson 1988, Folstad et al. 1989) or indirectly through increased nutritional costs associated with increased development of secondary sexual traits. Males demonstrate their genetic quality by the degree of development of secondary sexual characters and good physical condition during this period of reduced immunocompetence and elevated susceptibility to parasitism and disease (Zahavi 1975, Maynard Smith 1985, Folstad and Karter 1992). Theory predicts that females that choose mates with extravagant ornamentation will have greater fitness, and several studies have demonstrated

that offspring survival is greater when females mate with males that possess elaborate secondary characters (Norris 1993, Petrie 1994, von Schantz et al. 1994).

The major histocompatibility complex (MHC) likely plays a role in the “good genes” hypothesis (Howard 1991) because of its importance in antigen recognition and immune response. The MHC is a gene complex common to all vertebrates that serves to distinguish self from non-self. Class I and class II molecules of the MHC bind to antigens and aid in identifying foreign peptides (Klein 1986), thereby serving as the first line of defense in immune response to foreign pathogens (e.g., parasites and disease). While a plethora of studies have reported associations between the MHC and specific pathogens (malaria, tuberculosis, Lyme disease, etc.), our understanding of the associations of specific alleles and disease is poor. In addition, we have only begun to understand the influence that the MHC has on physiological processes such as growth, development, and reproduction. Development of secondary sexual characters, like other physiological processes, should benefit from MHC genes that confer an immunological advantage (Howard 1991), and relationships between certain alleles or genotypes of the MHC and degree of ornamentation likely exist in most species. von Schantz et al. (1996, 1997) found that spur length in male pheasants (*Phasianus colchicus*), a trait selected for by females (von Schantz et al. 1989), was associated with MHC genotype, but no other studies have documented similar relationships.

White-tailed deer (*Odocoileus virginianus*) are a polygonous species that annually develop extravagant ornamentation (e.g., antlers) that is important for intra- and intersexual displays. Because of the incredible nutritional demands that antler development places upon males each year (French 1956, Ullrey 1983, Asleson et al.

1997), we chose white-tailed deer as a model to test predictions of the Hamilton and Zuk (1982) handicap hypothesis and determine whether antler development is a good signal of genetic quality. Specifically, our objectives were to assess whether (1) MHC characteristics are associated with antler development and body size, (2) MHC characteristics are associated with circulating levels of testosterone, and (3) developmental traits of antlers are associated with parasite burdens in adult, male deer. Previous work (Ditchkoff unpubl. data) has demonstrated a significant association between the MHC and parasite burdens in white-tailed deer hosts, and suggested that particular allelic lineages may be important for providing resistance to potential pathogens.

Materials and Methods

We collected data from ($n = 128$) adult, male white-tailed deer that were harvested by hunters during October and November from 1995 to 1996 at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, USA (34°49'N, 95°55'W). The McAAP is an 18,212-ha area owned and operated by the U.S. Department of Defense, and has been managed to maintain a large proportion of mature males within the population (e.g., quality deer management) since 1989 (Ditchkoff et al. 1997). Vegetation on the area was characterized by oak uplands (*Quercus marilandica*, *Q. stellata*) and bottomlands (*Q. shumardii*, *Q. nigra*) intermixed with tallgrass prairie (*Andropogon virginicus*, *A. gerardii*, *Schizachyrium scoparium*) and shrub communities (*Smilax bonanox*, *Ulmus alata*, *Prunus angustifolia*, *Diospyros virginiana*). Soils tend to be sandy, and common soil series are Chateau very fine sandy loam, Dennis-Dwight complex, Eram clay loam, and Enders-Hector complex. Mean annual rainfall is 112 cm with a high mean

temperature of 28°C during July and low mean temperature of 4.5°C during December to February.

We measured chest girth immediately posterior to the front legs and body length from tip of the nose to 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 (tarsal). Skull length was measured as the tip of the nose to the base of the skull (occipital bone). Deer were weighed to the nearest 0.5 kg using a hanging scale immediately after they were field-dressed. We removed the testicles from the scrotum and weighed each to the nearest 0.1 g. Deer were aged by tooth wear and replacement (Severinghaus 1949).

To obtain a measure of antler size, we used the Boone and Crockett scoring method described by Nesbitt and Wright (1981). This system involves summing measurements (in inches) of main beam length, length of each tine, and circumferences of the main beam between successive tines (not to exceed 4 measured circumferences on each antler) to obtain a score for each antler. Each inch counts as a point in the scoring system. To calculate overall Boone and Crockett score, we summed antler scores for both left and right antlers and a measure of distance between the antlers (inside spread). All antler and body measurements were made using a 2-m flexible nylon tape.

We collected blood from the thoracic cavity of each deer into 10-ml evacuated serum-separating tubes (SST; Becton Dickinson Vacutainer Systems, Rutherford, NJ). Serum was separated by centrifugation within 6 h of collection and stored at -85°C. Serum testosterone levels were assayed with a direct RIA procedure (Coat-A-Count Testosterone, Diagnostics Products Corporation, Los Angeles, CA). Following the Coat-A-Count methodology, we added 50 μ l of serum and 1.0 ml of 125 I testosterone to

antibody-labeled tubes prior to incubation for 3 h at 37°C. Each Coat-A-Count tube was pre-labeled with monoclonal antibodies to testosterone. Following incubation, samples were thoroughly aspirated and radioactivity of tubes was counted in a gamma counter. Each sample was assayed in duplicate and samples with error >5% were reanalyzed. This assay is sensitive to testosterone concentrations ≥ 4 ng/dL, and interassay percentage CV is 5-12%.

When field-dressing deer, we removed the abomasum and tied both ends with string to avoid loss of contents. Abomasa were subsequently frozen until later analysis. In the laboratory, abomasal contents were removed, diluted with water to 1,000 ml, and a 50-ml aliquot examined under magnification (Prestwood et al. 1973). Total nematodes were calculated by multiplying the number of nematodes per aliquot by 20. Nematodes were identified according to Kubat et al. (1980). Ectoparasitic ticks (primarily *Amblyomma americanum* and *Ixodes scapularis*) were enumerated on the sternum of each deer prior to field-dressing using a template with a rectangular hole 2.5 x 12.5 cm. All ticks within the template were enumerated and the count was used as an index of the degree of infestation with ectoparasites.

We calculated abundance, intensity, and prevalence of each species of abomasal nematode according to Margolis et al. (1982). Abundance was defined as the mean number of abomasal nematodes per deer. We estimated intensity of infection by calculating mean number of nematodes per deer with ≥ 1 nematode, whereas prevalence was the percentage of deer with ≥ 1 nematode. For ticks, we calculated abundance only (not intensity or prevalence) because prevalence approached 100%.

Approximately 1 g of liver tissue was removed and placed in lysis buffer, and DNA was isolated following standard protocols (Longmire et al. 1997). We conducted polymerase chain reaction (PCR) amplification of *Mhc-DRB* exon 2 using primers LA31 and LA32 (Sigurdardottir et al. 1991). We identified allelic diversity of *Mhc-DRB* exon 2 using a modification of the single-stranded conformation polymorphism (SSCP) analysis described by Orita et al. (1989). We chose to study the *Mhc-DRB* because it is highly variable and has been the most widely studied MHC locus in white-tailed deer and *Artiodactyla* to date (Mikko and Anderson 1995, Swarbick et al. 1995, Mikko et al. 1997, Van Den Bussche et al. 1999). Van Den Bussche et al. (1999) provide a complete description of the genetic techniques employed for white-tailed deer.

Because relatively little is known about the MHC in white-tailed deer and other cervids, we felt any attempt to associate specific alleles with antler characteristics and testosterone levels would be premature. Instead, we classified alleles into 1 of 2 allelic lineages (Table 1) based upon earlier phylogenetic analyses (Van Den Bussche et al. 1999). Evolution of the MHC typically occurs from point mutations rather than recombination, resulting in lineages containing alleles that are likely similar from a functional standpoint. Using the phylogenetic classification we were then able to categorize the *Mhc-DRB* profiles of our deer into 3 categories. Deer with both *Mhc-DRB* alleles from lineage 1 were categorized as Type 11, and deer with both alleles from lineage 2 were categorized as Type 22. Deer with alleles from both lineages were categorized as Type 12.

We compared total Boone and Crockett score, antler score, number of points, beam length, and basal circumference of deer with different genetic types using analysis of

covariance (ANCOVA) with age as a covariate to control for age-related variation in antler size. We also used ANCOVA with age as a covariate to test for differences in body size between deer with different genetic types. We examined genetic influences on serum testosterone using ANCOVA with age and date of harvest as covariates. We tested for differences in least squared means to determine differences between genetic types if genetic effects were statistically significant ($P < 0.05$) in ANCOVAs. We used multiple regression to assess relationships between antler size and testosterone. Measures of antler size were the dependent variable and age was included with serum testosterone as an independent variable to control for age-related changes in antler size and testosterone. We used simple linear regression analyses to assess relationships between serum testosterone and parasite measures (e.g., abundance, intensity, and prevalence), and multiple regression to evaluate relationships between antler development and parasite burdens.

Results

We detected 15 alleles at *Mhc-DRB* and allelic frequencies ranged from 0.8 to 57.0% (Table 1). Type 11 deer accounted for 22% of the deer sampled, 37% of the deer were Type 12, and 41% of the deer were Type 22. Deer with *Mhc-DRB* alleles from both allelic lineage 1 and 2 (Type 12) had 20% and 13% greater ($P < 0.05$) gross Boone and Crockett antler scores than deer with *Mhc-DRB* Types 11 and 22, respectively (Table 2). Similarly, mean number of antler points and mean basal circumference were more than 14% and 8% greater ($P < 0.05$) for Type 12 deer than Types 11 or 22 deer, respectively. Type 12 deer had a 21% greater ($P < 0.05$) mean antler score and a 13% greater length of

main beams than Type 11 deer, but these antler traits did not differ from Type 22 deer. Although measures of antler size tended to be greater for Type 22 than Type 11 deer, statistical significance ($P > 0.05$) was not apparent. Field-dressed body mass and skull length were approximately 5% greater ($P < 0.05$) for Type 12 than Type 11 deer, but similar ($P > 0.05$) between Types 12 and 22 deer (Table 3). Body length, chest girth, and mean testicular mass did not differ ($P > 0.05$) among deer from the three MHC types.

Multiple regression analyses indicated that both age and testosterone were positively associated ($P < 0.05$) with and accounted for significant variation in antler characteristics (Table 4). Mean antler score increased 0.26 ± 0.09 (mean \pm SE) points, main beam length increased 0.16 ± 0.07 cm, number of antler points increased by 0.02 ± 0.01 , basal circumference increased 0.04 ± 0.01 cm, and Boone and Crockett score increased 0.57 ± 0.21 points for each mg/dL increase in serum testosterone. Regressions of Boone and Crockett score, mean antler score, main beam length, and basal circumference with age and testosterone produced $R^2 \geq 0.62$, while number of antler points had $R^2 = 0.48$ when regressed against age and testosterone. Concentrations of serum testosterone in deer with *Mhc-DRB* Type 12 were 75% greater ($P = 0.031$) than Type 22 deer (Fig. 1). Type 12 deer that were 2.5 years old also had greater ($P = 0.043$) concentrations of serum testosterone than 2.5-year old deer from with Type 22 genetics. This trend was not apparent in other age classes. Concentrations of serum testosterone in Type 11 deer did not differ ($P > 0.05$) from those deer with Type 12 or Type 22 genetic characteristics within age classes or overall.

Total abundance of abomasal nematodes was 735.7 ± 52.7 with abundance estimates ranging from 20 to 3,200 nematodes. We identified 6 species of abomasal

nematodes; *Haemonchus contortus* ($x = 25.8 \pm 11.0$), *Apteragia odocoilei* ($x = 504.0 \pm 35.0$), *A. pursglovei* ($x = 3.3 \pm 1.5$), *Ostertagia dikmansi* ($x = 148.3 \pm 16.7$), *O. mossi* ($x = 58.4 \pm 9.8$), and *O. ostertagia* ($x = 3.0 \pm 1.6$). Statistical analysis of *A. pursglovei* and *O. ostertagia* was not possible because each were found in <5 deer. Mean number of nematode species within the abomasum of each deer was 2.6.

Abundances of total abomasal nematodes ($P = 0.934$), *H. contortus* ($P = 0.564$), *A. odocoilei* ($P = 0.368$), *O. mossi* ($P = 0.174$), *O. dikmansi* ($P = 0.738$), and sternum ticks ($P = 0.367$) were not associated with levels of serum testosterone. Similarly, intensity or prevalence of infection ($P > 0.05$) were not associated with levels of serum testosterone. In contrast, multiple regression analysis revealed that total abundance of abomasal nematodes was negatively associated ($P = 0.050$) with mean antler score (Table 5). However, individual species of nematodes were not associated ($P > 0.05$) with antler size. Our index of ectoparasitic ticks was positively associated with antler size ($P = 0.033$) and body mass ($P = 0.001$).

Discussion

We observed significant associations of the MHC with secondary sexual character (e.g., antlers) development in white-tailed deer. Deer that possessed *Mhc-DRB* alleles from both evolutionary clades (Type 12 deer) generally had greater age-adjusted development of antlers. Previous studies using electrophoretic analysis have suggested that heterozygosity at select protein-generating loci is associated with increased development of antlers (Smith et al. 1983; Scribner et al. 1984, 1989; Scribner and Smith 1990) and growth of other tissues (Chesser and Smith 1987) in deer. However, our

observations provide the first evidence that the MHC is potentially associated with antler development. von Schantz et al. (1996, 1997) observed an association between MHC genotype and spur length in pheasants, but additional insights into MHC-driven development of secondary sexual characters have yet to be reported.

According to the Hamilton and Zuk (1982) hypothesis regarding expression of condition-dependent male traits, development of large antlers should be driven by genetic advantages that result in superior condition. While degree of antler development represents a male's ability to allocate energy and nutrients to antler growth during the previous year, other morphological measures are more representative of an individual's condition over the course of their life. We found that deer with alleles from both evolutionary clades of the *Mhc-DRB* (Type 12) had greater body mass and skull length than Type 11 deer. These relationships suggest that heterozygosity within the MHC of white-tailed deer may be an important determinant of fitness through its influence on nutritional condition and ultimately reproductive success. Previous work has indicated that body mass and antler size are important criteria for establishing dominance and maximizing mating success in Cervids (Townsend and Bailey 1981, Clutton-Brock et al. 1982). As a result, male white-tailed deer with *Mhc-DRB* heterozygosity, through greater resource allocation to body growth and antler development, may maximize their potential lifetime fitness.

Antler development, according to the predictions of Hamilton and Zuk (1982), should serve as a signal of genetic quality to females by demonstrating the ability of males to cope with immunosuppression. Although most models of the Hamilton and Zuk (1982) theory propose testosterone-driven immunosuppression as an advertisement of genetic

quality (Ligon et al. 1990, Folstad and Karter 1992), the nutritional stress that antler development imposes upon male deer may serve as equally an impressive signal to females as hormonal-mediated immunosuppression. The importance of nutrition to antler development and body condition in deer is well documented (French et al. 1956, Ullrey 1983, Asleson et al. 1997), and it is probable that the extreme nutritional requirements imposed by antler growth may compete for resources required by a functioning immune system (Lochmiller and Deerenberg 1999). As a result, by developing large antlers, male deer demonstrate their genetic quality to potential mates by maintaining good health during a potentially stressful period of their life history. We posit that deer with greater genetic heterozygosity of the MHC are better able to cope with the various nutritional stresses associated with antler development, and advertise their ability by maximizing antler development.

Circulating levels of testosterone, like antler development, also serve to advertise genetic quality to potential mates during the breeding season through development of secondary sexual characters and modifications in behavior. Testosterone is important in stimulating reproductive behavior of most species during the breeding season, and the literature is replete with information documenting increases in displays and aggressive reproductive behaviors following testosterone supplementation (Ketterson and Nolan 1992). In white-tailed deer, testosterone has been found to be important for expression of rutting behaviors such as rubbing, scraping, and sparring, and ultimately establishing dominance (Miller et al. 1987). The physical stresses resulting from this testosterone-mediated activity commonly result in elevated levels of mortality for male deer during and immediately following the breeding season (Clutton-Brock et al. 1982, Gavin et al. 1984).

Because of the stresses placed upon male deer during the rut and the positive association that testosterone has on rutting behaviors, we would expect testosterone levels to be influenced by a deer's capacity to cope with stress. Ligon et al. (1990) stated that testosterone acts to channel physical condition into external advertisements of condition, thus individuals in good condition should have the greatest levels of testosterone. Our data support this idea by showing that deer with greater *Odvi-DRB* heterozygosity (Type 12) had levels of serum testosterone that were up to 75% greater than deer that possessed both *Odvi-DRB* alleles from the same evolutionary clade.

The "good genes" theory predicts that highly ornamented males should have the lowest parasite burdens because of genetic quality. We found that total abundance of abomasal nematodes was negatively correlated with antler size when controlling for age, suggesting that antlers can serve as an honest advertisement of quality to potential mates. Although we did not detect significant relationships between abundances of specific species of nematodes and antler size, there tended to be negative relationships for all species. Similar relationships have been reported for red jungle fowl (*Gallus gallus*), where males experimentally infected with an intestinal nematode had duller combs and hackle feathers, and shorter combs and tail feathers than control males (Zuk et al. 1990a, 1990b). Saino et al. (1995) found that ectoparasite infestation was negatively correlated with tail length in the barn swallow (*Hirundo rustica*), and Watve and Sukumar (1997) reported that tusk length in male Asian elephants (*Elaphus maximus*) was negatively associated with intestinal parasite load. Contrary to our intestinal helminth data, ectoparasitic ticks were positively correlated with antler size. We also detected a positive association between density of ectoparasitic ticks and body mass, and previous work has

demonstrated that density of ectoparasites increases as host body size increases in African ungulates (Mooring and Mundy 1996, Gallivan and Horak 1997). We hypothesize that the positive relationship we detected between antler size and parasite density is an artifact of body size and results from colinearity of body mass and antler development.

We anticipated that testosterone levels would positively influence parasite loads because of the immunosuppressive properties of androgenic hormones (Grossman 1985, Folstad et al. 1989, Saino et al. 1995), but the timing of our sampling may have precluded the detection of any potential relationships. Testosterone levels begin to rise during August-September and peak during October-November (Bubenik 1983) in white-tailed deer, the period during which we collected samples. If there is a lag in parasite response to rising systemic testosterone, then we may have collected many of our samples before testosterone-parasite relationships became detectable.

Our observations suggest that mate selection in white-tailed deer is consistent with the immunocompetence handicap hypothesis. Males possessing *Odvi-DRB* alleles from different lineages tended to have greater antler development and body size than deer with 2 alleles from the same lineage, suggesting that an indirect association between the MHC and sexual advertisement may exist. Additionally, the MHC was associated with testosterone levels during the breeding season, which in turn are positively related to antler development and breeding effort. High testosterone levels are indicative of deer that are in good condition and can cope with the stresses imposed by extensive breeding activity and subsequent pathogenic challenges. Parasite burdens tended to be lower among large antlered deer, providing support for the hypothesis that antlers are a signal of male genetic quality.

It is not our intention to suggest that the MHC codes for antler development or body size, but rather that general characteristics of the MHC may be evident in phenotypic expression of adult, male white-tailed deer. We have briefly described the pathways by which the MHC could influence physical characteristics or hormone levels in deer in an attempt to illustrate the indirect effects that the MHC may have on secondary sexual character development, and ultimately sexual advertisement. Undoubtedly, further work is needed to improve our understanding of genetic advertisement through phenotypic expression. Specifically, we should focus on improving our understanding of how the MHC affects condition so that we can better understand the indirect manner in which the MHC influences sexual advertisement.

Literature Cited

- Adkins-Regan, R. 1981. Hormone specificity, androgen metabolism, and social behavior. *Am. Zool.* 21:257-271.
- Alexander, J., and W. H. Stimson. 1988. Sex hormones and the course of parasitic infection. *Parasitol. Today* 4:189-193.
- Asleson, M. A., E. C. Hellgren, and L. W. Varner. 1997. Effects of seasonal protein restriction on antlerogenesis and body-mass in adult, male white-tailed deer. *J. Wildl. Manage.* 61:1098-1107.
- Bubenik, G. A. 1983. The endocrine regulation of the antler cycle. Pp. 73-107 in R. D. Brown, ed. *Antler development in Cervidae*. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.

- Chesser, R. K., and M. H. Smith. 1987. Relationships of genetic variation to growth and reproduction in white-tailed deer. Pp. 168-177 in C. M. Wemmer, ed. Biology and management of the Cervidae. Smithsonian Institution Press, Washington, DC.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, IL.
- Ditchkoff, S. S., E. R. Welch, Jr., W. R. Starry, W. C. Dinkines, R. E. Masters, and R. L. Lochmiller. 1997. Quality deer management at the McAlester Army Ammunition Plant: a unique approach. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 51:389-399.
- Folstad, I., and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139:603-622.
- Folstad, I., A. C. Nilssen, O. Halvorsen, and J. Andersen. 1989. Why do male reindeer (*Rangifer t. tarandus*) have higher abundances of second and third instar larvae of *Hypoderma tarandi* than females? Oikos 55:87-92.
- French, C. E., L. E. McEwen, N. D. Magruder, R. H. Ingram, and R. W. Swift. 1956. Nutrient requirements for growth and antler development in the white-tailed deer. J. Wildl. Manage. 20:221-232.
- Gallivan, G. J., and I. G. Horak. 1997. Body-size and habitat as determinants of tick infestations of wild ungulates in South Africa. S. Afr. J. Wildl. Res. 27:63-70.
- Gavin, T. A., L. H. Suring, P. A. Vohs, Jr., and E. C. Meslow. 1984. Population characteristics, spatial organization, and natural mortality in the Columbian white-tailed deer. Wildl. Monogr. 91:1-41.

- Grossman, C. J. 1984. Regulation of the immune system by sex steroids. *Endocr. Rev.* 5:435-455.
- 1985. Interactions between the gonadal steroids and the immune system. *Science* 227:257-261.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384-387.
- Howard, J. C. 1991. Disease and evolution. *Nature*. 352:565-567.
- Ketterson, E. D., and V. Nolan, Jr. 1992. Hormones and life histories: an integrative approach. *Am. Nat.* 140:S33-S62.
- Klein, J. 1986. Natural history of the major histocompatibility complex. John Wiley and Sons, New York, NY.
- Kubat, G., A. A. Kocan, and W. R. Davidson. 1980. Identification of abomasal parasites of white-tailed deer. *Wildl. Dis. Assoc.*, Ames, IA.
- Ligon, J. D., R. Thornhill, M. Zuk, and K. Johnson. 1990. Male-male competition, ornamentation, and the role of testosterone in sexual selection in red jungle fowl. *Anim. Behav.* 40:367-373.
- Lochmiller, R. L., and C. Deerenberg. 1999. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos*. In press.
- Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of "lysis buffer" in DNA isolation and its implications for museum collections. *Occas. Papers, The Museum, Texas Tech Univ., Lubbock* 163:1-3.

- Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *J. Parasitol.* 68:131-133.
- Maynard Smith, J. 1985. Mini review: sexual selection, handicaps and true fitness. *J. Theor. Biol.* 115:1-8.
- Mikko, S., and L. Andersson. 1995. Low major histocompatibility complex class II diversity in European and North American moose. *Proc. Natl. Acad. Sci. USA* 92:4259-4263.
- Mikko, S., H. A. Lewin, and L. Anderson. 1997. A phylogenetic analysis of cattle *DRB3* alleles with a deletion of codon 65. *Immunogenetics* 47:23-29.
- Miller, K. V., R. L. Marchinton, K. J. Forand, and K. L. Johansen. 1987. Dominance, testosterone levels,, and scraping activity in a captive herd of white-tailed deer. *J. Mammal.* 68:812-817.
- Mooring, M. S., and P. J. Mundy. 1996. Factors influencing host selection by yellow-billed oxpeckers at Matobo National-Park, Zimbabwe. *Afr. J. Ecol.* 34:177-188.
- Morris, J. M., and G. A. Bubenik. 1982. The effects of androgens on the development of antler bone. Pp. 123-141 *in* R. D. Brown, ed. *Antler development in Cervidae*. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.
- Nesbitt, W. H., and P. L. Wright. 1981. *Records of North American big game*. The Boone and Crockett Club, Alexandria, VA.
- Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* 362: 537-539.

- Orita, M., H. Iwahana, H. Kanazawa, K. Hayashi, and T. Sekiya. 1989. Detection of polymorphisms of human DNA by gel electrophoresis as single-stranded conformation polymorphisms. *Proc. Natl. Acad. Sci. USA* 86:2766-2770.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* 371, 598-599.
- Prestwood, A. K., F. A. Hayes, J. H. Eve, and J. F. Smith. 1973. Abomasal helminths of white-tailed deer in southeastern United States, Texas, and the Virgin Islands. *J. Am. Vet. Med. Assoc.* 163: 556-561.
- Saino, N., A. P. Møller, and A. M. Bolzern. 1995. Testosterone effects on the immune system and parasitic infestations in the barn swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. *Behav. Ecol.* 6:397-404.
- Scribner, K. T., and M. H. Smith. 1990. Genetic variability and antler development. Pp. 460-473 *in* G. A. Bubenik and A. B. Bubenik, eds. *Horns, pronghorns, and antlers*. Springer-Verlag, New York, NY.
- Scribner, K. T., M. H. Smith, and P. E. Johns. 1984. Age, condition, and genetic effects on incidence of spiked bucks. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* 38:23-32.
- , 1989. Environmental and genetic components of antler growth in white-tailed deer. *J. Mammal.* 70:284-291.
- Severinghaus, C. W. 1949. Tooth development and wear as criteria for age in white-tailed deer. *J. Wildl. Manage.* 13:195-216.

- Sigurdardottir, S., C. Borsch, K. Gustaffson, and L. Andersson. 1991. Cloning and sequence analysis of 14 *DRB* alleles of the bovine major histocompatibility complex by using the polymerase chain reaction. *Anim. Genet.* 22:199-209.
- Silverin, B. 1980. Effects of long-acting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*. *Anim. Behav.* 28:906-912.
- Smith, M. H., R. K. Chesser, E. G. Cothran, P. E. Johns. 1983. Genetic variability and antler growth in a natural population of white-tailed deer. Pp. 365-388 in R. D. Brown, ed. *Antler development in Cervidae*. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.
- Swarbick, P. A., F-W. Schwaiger, J. T. Epplen, G. S. Buchan, J. F. T. Griffith, and A. M. Crawford. 1995. Cloning and sequencing of expressed *DRB* genes of the red deer (*Cervus elaphus*) Mhc. *Immunogenetics* 42:1-9.
- Townsend, T. W., and E. D. Bailey. 1981. Effects of age, sex and weight on social rank in penned white-tailed deer. *Am. Mid. Nat.* 106:92-101.
- Ullrey, D. E. 1983. Nutrition and antler development in white-tailed deer. Pp. 49-60 in R. D. Brown, ed. *Antler development in Cervidae*. Caesar Kleberg Wildl. Res. Inst., Kingsville, TX.
- Van Den Bussche, R. A., S. R. Hooper, and R. L. Lochmiller. 1999. Characterization of *Mhc-DRB* allelic diversity in white-tailed deer (*Odocoileus virginianus*) provides insight into *Mhc-DRB* allelic evolution in Cervidae. *Immunogenetics* 49:429-437.
- von, Schantz, T., G. Göransson, G. Andersson, I. Fröberg, M. Grahn, A. Helgeé, and H. Witzell. 1989. Female choice selects for a viability-based male trait in pheasants. *Nature*. 337:166-169.

- von, Schantz, T., M. Grahn, and G. Göransson. 1994. Intersexual selection and reproductive success in the pheasant *Phasianus colchicus*. *Am. Nat.* 144:510-527.
- von, Schantz, T., H. Wittzell, G. Göransson, and M. Grahn. 1997. Mate choice, male condition-dependent ornamentation and MHC in the pheasant. *Hereditas* 127:133-140.
- von, Schantz, T., H. Wittzell, G. Göransson, M. Grahn, and K. Persson. 1996. MHC genotype and male ornamentation: genetic evidence for the Hamilton-Zuk model. *Proc. R. Soc. Lond. B* 263:265-271.
- Watve, M. G., and R. Sukumar. 1997. Asian elephants with longer tusks have lower parasite loads. *Curr. Sci.* 72:885-889.
- Zahavi, A. 1975. Mate selection - a selection for a handicap. *J. Theor. Biol.* 53:205-214.
- Zuk, M., K. Johnson, R. Thornhill, and J. D. Ligon. 1990a. Parasites and male ornaments in free-ranging and captive red jungle fowl. *Behaviour* 114:232-248.
- Zuk, M., R. Thornhill, and J. D. Ligon. 1990b. Parasites and mate choice in red jungle fowl. *Am. Zool.* 30:235-244.

Table 1. Categorization of alleles of the *Mhc-DRB* (*Odvi*) exon 2 found in white-tailed deer from southeastern Oklahoma, USA, into evolutionary lineages based upon phylogenetic analysis^a.

Allelic lineage 1	Frequency (%)	Allelic lineage 2	Frequency (%)
<i>Odvi-DRB*01</i>	3.9	<i>Odvi-DRB*02</i>	0.8
<i>Odvi-DRB*03</i>	3.9	<i>Odvi-DRB*05</i>	57.0
<i>Odvi-DRB*04</i>	42.2	<i>Odvi-DRB*06</i>	1.6
<i>Odvi-DRB*09</i>	1.6	<i>Odvi-DRB*07</i>	28.1
<i>Odvi-DRB*13</i>	1.6	<i>Odvi-DRB*08</i>	2.3
<i>Odvi-DRB*14</i>	14.1	<i>Odvi-DRB*10</i>	3.1
<i>Odvi-DRB*15</i>	0.8	<i>Odvi-DRB*11</i>	10.9
		<i>Odvi-DRB*12</i>	8.6

^a Evolutionary groupings were based upon phylogenetic analysis of Van Den Bussche et al. (1999).

Table 2. Least square means of antler measurements from white-tailed deer with different *Mhc-DRB* (*Odvi*) characteristics calculated from an analysis of covariance with age as a covariate.

<i>Odvi-DRB</i>	Gross Boone and Crockett score	Mean antler score	Mean number of antler points	Mean main beam length (cm)	Mean basal circumference (cm)
Type 11	69.0 a ^a	28.9 a	2.95 a	32.7 a	7.55 a
Type 12	83.0 b	34.9 b	3.46 b	36.9 b	8.25 b
Type 22	73.7 a	31.4 ab	3.03 a	34.0 ab	7.61 a

^a Least square means in a column with different letters are different ($P \leq 0.05$).

Table 3. Least square means of body measurements from white-tailed deer with different *Mhc-DRB* (*Odvi*) characteristics calculated from an analysis of covariance with age as a covariate.

<i>Odvi-DRB</i>	Field-dressed body mass (kg)	Body length (cm)	Skull length (mm)	Chest girth (mm)	Testicle mass (g)
Type 11	44.5 a ^a	133.3 a	309.3 a	870.9 a	36.0 a
Type 12	47.9 b	135.8 a	324.0 b	870.9 a	36.4 a
Type 22	45.7 ab	134.5 a	317.2 ab	814.6 a	32.7 a

^a Least square means in a column with different letters are different ($P \leq 0.05$).

Table 4. Parameter estimates of multiple regressions comparing age and concentration of serum testosterone to measures of antler size in male white-tailed deer ($n = 128$) from a population in southeastern Oklahoma, USA.

Dependent variable	R^2	Intercept			Age (years)			Testosterone (ng/dL)		
		Est.	SE	P	Est.	SE	P	Est.	SE	P
Antler score ^a	0.63	7.47	1.93	0.001	8.44	0.63	0.001	0.26	0.09	0.007
Beam length	0.62	16.02	1.49	0.001	6.51	0.48	0.001	0.16	0.07	0.028
Antler points	0.48	1.46	0.19	0.001	0.60	0.06	0.001	0.02	0.01	0.016
Basal circum.	0.66	4.34	0.26	0.001	1.21	0.08	0.001	0.04	0.01	0.001
B & C score ^b	0.63	20.08	4.26	0.001	18.87	1.39	0.001	0.57	0.21	0.008

^a Antler score was determined as the mean of individual Boone and Crockett scores (Nesbitt and Wright 1981) for each antler.

^b Boone and Crockett scores were measured according to Nesbitt and Wright (1981).

Table 5. Parameter estimates of multiple regressions comparing age and parasite abundance of select species to mean antler score (dependent variable) of white-tailed deer from a population in southeastern Oklahoma, USA.

Species	Parasite abundance (number/host)			Age (years)			Intercept			R^2
	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>	Est.	SE	<i>P</i>	
<i>H. contortus</i>	-0.33	0.26	0.202	8.79	0.68	0.001	8.7	2.3	0.001	0.61
<i>A. odocoilei</i>	-0.17	0.13	0.211	9.00	0.67	0.001	11.0	3.4	0.001	0.61
<i>O. mossi</i>	-0.20	0.19	0.287	8.81	0.86	0.001	9.9	3.5	0.006	0.59
<i>O. dikmansii</i>	-0.55	0.22	0.815	8.99	0.85	0.001	7.6	2.8	0.009	0.58
Total ^a	-0.22	0.11	0.050	8.96	0.66	0.001	13.3	3.5	0.001	0.61
Ticks ^b	0.08	0.04	0.033	9.31	0.72	0.001	4.6	2.1	0.032	0.66

^a Total abomasal parasites.

^b Index of ectoparasitic ticks measured by enumerating ticks within a specified area of the sternum.

CHAPTER IV

AGE-SPECIFIC PATTERNS OF MORTALITY AMONG MALE WHITE-TAILED DEER SUPPORT MATE COMPETITION THEORY

Summary

Mate competition theory predicts that males will invest resources toward intrasexual competition for mates until reproductive benefits are outweighed by costs to future fitness. In populations that have a substantial proportion of mature males, theory predicts that young males will forego reproduction to reduce exposure to mortality that may result from breeding efforts. We examined age-specific mortality of males in a white-tailed deer (*Odocoileus virginianus*) population in which >50% of the males were ≥ 3.5 years old to determine whether male patterns of mortality conform to mate competition theory. Annual mortality rates were relatively stable throughout adulthood (0.26 - 0.38), but causes of mortality changed with age. Young males (1.5-2.5 years old) were most susceptible to human-induced mortality (e.g., hunting and vehicle accidents), while males ≥ 3.5 years old tended to die from natural causes more frequently than younger deer. Proportional hazard models also indicated that as antler size increased, likelihood of mortality increased. Age- and cause-specific patterns of mortality in adult, male white-tailed deer from a population with at least 50% mature males mirror patterns predicted by mate competition theory.

Introduction

Mate competition theory states that populations with a substantial proportion of mature males should possess mating systems dominated by mature males. Young males in these populations should forego reproduction early in life because of the low probability of successfully acquiring a mate, and their strategy is likely based upon the expected costs of mate competition and probability of success. Although young males that commit significant resources to mate competition may increase current reproductive success, they may jeopardize lifetime reproductive success because of decreased probability of survival in the future (Geist 1971). Clutton-Brock et al. (1982) found that reproduction in red deer (*Cervus elaphus*) populations was dominated by mature males, and similar findings have been reported for pronghorn antelope (*Antilocapra americana*; Byers 1997). White-tailed deer (*Odocoileus virginianus*) populations have been subjected to extensive hunting pressures across most of their range in recent decades, resulting in demographic conditions, such as younger age distributions, that differ from those in which they evolved (Miller et al. 1995). It has been postulated that young males in these populations exert greater reproductive effort than in populations that have greater numbers of mature males (Miller and Marchinton 1995). However, the paucity of older-aged populations has resulted in few investigations of the reproductive strategies of male white-tailed deer in populations that have a substantial proportion of mature males.

We examined mortality patterns of male white-tailed deer in a population with a large proportion of mature males to improve our understanding of the reproductive strategies of males under these demographic conditions. We hypothesized that if younger

males were committing less resources to breeding or competition for mates than mature males, they would not be as susceptible to the natural mortality agents that often plague mature deer following the breeding season. We also postulated that probability of mortality would be related to morphological and physiological characteristics of deer. Specifically, we predicted that increased body size and antler development, traits associated with reproductive success (Clutton-Brock et al. 1982), would be associated with increased competition for mates and subsequently result in greater mortality.

Materials and Methods

The study was conducted at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, USA. The McAAP is an ammunition production and storage facility that is owned and operated by the U.S. Department of Defense. Public access on the area is restricted. The McAAP encompasses 18,212 ha, 98.6% of which is composed of native vegetation. The area consists of post oak (*Quercus stellata*) - blackjack oak (*Q. marilandica*) uplands with understories of greenbriar (*Smilax bona-nox*), buckbrush (*Symphoricarpos orbiculatus*), and poison ivy (*Toxicodendron radicans*), and riparian drainages of mainly water oak (*Q. nigra*), red oak (*Q. shumardii*), and bur oak (*Q. macrocarpa*) overstories with buckbrush, greenbriar, and broadleaf uniola (*Chasmanthium latifolium*) understories. Large areas of native prairie grasses, including broomsedge bluestem (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), and panicums (*panicum* spp.), are maintained as hay meadows and are bisected by brushy draws consisting of winged elm (*Ulmus alata*), sumac (*Rhus* spp.), sand plum (*Prunus angustifolia*), hackberry (*Celtis* spp.), persimmon (*Diospyros virginiana*), osage orange

(*Maclura pomifera*), and honey locust (*Gleditsia triacanthos*). Approximately 200 ha of food plots planted with a mixture of rye, wheat, and clover are dispersed over much of the area.

The McAAP has been open to public hunting via lottery since 1962 but has been managed under the objectives of quality deer management since 1989 (Ditchkoff et al. 1997). As a result, the male segment of the herd on McAAP contains $\geq 50\%$ mature (≥ 3.5 years old) deer (Ditchkoff et al. 2000), which is uncommon across most of their range (Miller and Marchinton 1995). The primary mechanism used to limit hunter success and maintain a suitable proportion of mature deer in the population is the limitation of hunters to traditional archery equipment (e.g., recurve or longbows). Hunter success at the McAAP has averaged about 10% since inception of the traditional archery rule (Ditchkoff et al. 1996), thereby creating a scenario where natural mortality factors are as important in driving herd demographics as hunting pressure.

We captured adult (≥ 1.5 years of age) male white-tailed deer during December 1994-January 1995 ($n = 50$), January 1996 ($n = 13$), and January 1997 ($n = 17$) using drop-nets (Ramsey 1968) on food plots prebaited with whole corn and persimmons. Captured deer were aged by tooth wear and eruption (Severinghaus 1949) and fitted with radiocollars (Advanced Telemetry Systems, Inc., Isanti, Minnesota). Each radiocollar was equipped with a 4-hour mortality sensor that was triggered whenever the radiocollar was stationary for a period >4 hours. Prior to release, we measured chest girth, body length, and antler characteristics. We calculated a Boone and Crockett score for each set of antlers to estimate antler size by summing of measurements (inches) of beam length, all tines, greatest inside spread, and 4 circumferences of the main beam: each inch counted as

a point using this scoring system (Nesbitt and Wright 1981). We enumerated ectoparasitic ticks on the sternum within a 5- x 25-cm template. We also collected whole blood via jugular venipuncture into a 10-ml, evacuated, serum-separating tube (SST---Becton Dickinson Vacutainer Systems, Rutherford, New Jersey). Serum was separated from blood by centrifugation and stored at -80°C. Serum was analyzed for blood urea nitrogen (BUN), total protein, creatinine phosphokinase (CPK), and albumin (Vet-Pro Labs, Tulsa, Oklahoma).

Cause-specific mortality was determined by locating dead deer and performing in-field necropsies. Evidence such as presence of predators or scavengers, hunting wounds, and condition assessment (femur marrow fat, etc.) was used to determine cause of death. We classified mortalities due to hunting, poaching, and vehicular collisions as human-induced and all others as natural. If a specific cause of death could not be determined, it was classified as unknown. However, in all cases where mortality was classified as unknown, we were able to rule out human-induced mortality and thus categorized these as natural mortality. All deer harvested were brought to a check station so we were aware of all study deer that were legally harvested.

We determined Kaplan-Meier estimates of annual survival (1 Apr – 31 Mar) and compared survival curves between age classes using PROC LIFETEST (Allison 1995; SAS Institute Inc. 1988) because that procedure allowed for a staggered-entry design (Pollock et al. 1989). We separated animals into 3 age classes; 1.5-2.5 years old, 3.5-4.5 years old, and ≥ 5.5 years old. Antler development in white-tailed deer >5.5 years-old is approaching maximum, and deer <3.5 years-old, although morphologically mature, lack significant antler development and are commonly classified as immature. Animals were

classified into age classes based upon their age in November. Animals were considered to be 1 year older on 1 April. Annual probability of survival was compared between age classes using Z-tests (Heisey and Fuller 1985), and survival curves were compared with Wilcoxon and log-rank tests (SAS Institute Inc. 1988). Program MICROMORT (Heisey 1985) was used to calculate the probability of mortality due to specific causes. We used proportional hazard models (Allison 1995; Cox 1972) to determine how morphological and physiological parameters influenced the likelihood of overall and human-induced mortality during the year following capture. Unlike traditional survival analyses, proportional hazard models do not calculate probability of survival or mortality, but rather estimate how mortality rates change according to changes among independent variables. We did not examine natural mortality with hazard models because there were only 2 mortalities due to natural causes during the year following capture. The study ended on 31 December 1997.

Results

During the study, there were 45,465 deer-radio days and 39 documented mortalities. Greatest annual probability of mortality was due to hunting ($P_m = 0.124$), followed by vehicle collisions ($P_m = 0.021$), poaching ($P_m = 0.021$), and predation ($P_m = 0.021$; Table 1). Eight mortalities were classified as unknown because we could not determine a specific cause of death, and 4 additional mortalities that could not be easily categorized were classified as other. Probability of mortality from all natural causes was 0.104 and human-induced causes was 0.166. Annual probability of survival for adult male deer was 0.68 with the majority (72%) of mortalities occurring during or immediately

following the breeding season (1 Oct-15 Dec; Fig. 1). We did not detect differences ($P > 0.20$) in overall survival (curve shape or endpoint) between age classes (Fig. 2), suggesting that seasonal differences in survival between age classes were absent.

Young males (≤ 2.5 years old) were nearly 5 times as likely ($P = 0.042$) to die from human-induced causes ($P_m = 0.133$) than natural factors ($P_m = 0.027$; Table 2). In contrast, deer > 5.5 years old had human-induced and natural mortality estimates ($P_m = 0.133$) that were equal. Although human-induced mortality ($P_m = 0.209$) for deer 3.5-4.5 years old tended to be greater than natural mortality ($P_m = 0.129$), the estimates were not statistically different ($P = 0.114$). Young males (1.5-2.5 years old) were less likely to die from natural causes than deer 3.5-4.5 years old ($P = 0.020$) or deer > 5.5 years old ($P = 0.031$). However, probability of mortality due to human-induced agents did not vary between age classes ($P \geq 0.145$).

Proportional hazard models indicated that a 1-year increase in age resulted in a 64% decrease ($P = 0.010$) in likelihood of mortality due to any cause during the year following capture (Table 3). Antler size and density of sternum ticks both had a positive effect ($P < 0.05$) on likelihood of mortality due to all causes during the year following capture. As antler score increased by 10-points, there was a predicted increase in probability of mortality of 0.240, and probability of mortality was predicted to increase by 0.110 with each additional tick on the sternum. When examining only human-induced mortalities, hazard models indicated that a 1-year increase in age resulted in a 98% decrease in the likelihood of dying due to human-induced factors. Antler size, tick numbers, and CPK concentration were associated positively ($P < 0.05$) with the likelihood of dying due to human-induced factors during the year following capture.

Discussion

Kaplan-Meier survival estimates suggested that mortality rates in our population of white-tailed deer were relatively constant among age classes of adults. This is similar to results reported by Kie and White (1985) who found that survival rates of deer were independent of age between juvenile and senescent stages, although Klein and Olson (1960) reported that black-tailed deer (*O. hemionus sitkensis*) in Alaska had increased mortality at ages >5 years. Proportional hazard models seemed to contradict the results of the Kaplan-Meier estimates by indicating that there was a substantial decrease in the likelihood of mortality during the year following capture with each 1-year increase in age. However, it should be noted that hazard models do not calculate probability of survival like Kaplan-Meier estimates, but rather estimate the effect that specific variables have on survival by calculating how risk of mortality (risk ratio) changes with each variable (Allison 1995). In addition, the majority of mortalities (90.5%) that were used for hazard model calculations were human-induced mortalities; thus, age-specific differences in probability of mortality due to human-induced factors could introduce bias if hazard models were used to predict the effects of age on overall survival.

While our data suggest that overall survival rates of male deer in our population were consistent throughout adulthood, susceptibility to specific mortality agents changed with age. We found that deer ≥ 3.5 years of age were more susceptible to natural mortality than younger adults (1.5-2.5 years of age), and these mortalities usually followed the breeding season. In ungulate populations where there are a large proportion of mature males, such as on our study area where $\geq 50\%$ of the males are ≥ 3.5 years old (Ditchkoff

et al. 2000), competition for mates can be intense and energy expenditure great, resulting in increased levels of natural mortality (Clutton-Brock et al. 1982; Klein and Olson 1960; Robinette et al. 1957). Owen-Smith (1993) and Byers (1997) described this elevated mortality as senescence, but it should be considered increased exposure to mortality due to behavioral factors rather than physiological deterioration caused by aging. Males that invest significant resources in competition for mates increase their exposure to natural mortality agents (e.g., malnutrition, exhaustion). Although some types of natural mortality may not be linked directly to mate competition, most types of natural mortality can usually be attributed to physical exhaustion and poor nutritional intake, which are common in male cervids following the breeding season (Klein and Olson 1960). Young males in populations where there are a large proportion of mature deer probably do not fully participate in rut-related activities and, thus are not as susceptible to natural mortality agents because of superior condition (Miller and Marchinton 1995). We did not detect an increase in mortality during late adulthood that we would attribute to senescence.

In contrast to older adults, young adults (1.5-2.5 years of age) were more susceptible to human-induced mortality agents, and according to our proportional hazard model, there was a 98% decrease in the likelihood of a deer succumbing to human-induced mortality during the year following capture with each 1-year increase in age. Elevated susceptibility of young adults to human-induced mortality agents is probably due to lack of experience. These data are not without precedence because young adults commonly are over-represented in hunter-harvest data (Dasmann and Taber 1956; McCullough 1979; Roseberry and Klimstra 1974). Holzenbein and Marchinton (1992) attributed elevated mortality in young, dispersing deer to inexperience and unfamiliarity

with new areas and noted that human-induced mortality factors were very important. In contrast to young males, mature deer have substantially more experience in eluding hunters and safely traversing roads and thus are probably less susceptible to human-induced mortality agents.

Proportional hazard models also suggested that antler size and an index of tick infestation may influence the likelihood of mortality due to all causes during the year following capture. Because hazard models calculate risk ratios for each variable while controlling for all other variables (Allison 1995) and age was included as a variable in the model, we can draw inferences to how antler size and parasites affect survival within an age class. Elevated antler development can be viewed as an investment towards reproduction, and individuals with increased antler development may be more likely to participate in rut-related activities than counterparts with smaller antlers because of improved chances of success. Thus, if large antlered deer are more likely to participate in mate competitions, then we would expect probability of mortality to increase as antler size increases, assuming no changes in age, because of the increased likelihood of mortality from energetic rigors associated with breeding (Clutton-Brock et al. 1982; Klein and Olson 1960). Similarly, parasites (e.g. ticks) have negative effects on the condition of deer (see Davidson 1981), and thus we would expect to find increases in the likelihood of mortality as parasite loads increase.

Contrary to our original expectations, we did not detect an association between body size and mortality. Indices of body size normally are associated positively with antler development in cervids (Harmel 1983), and antler development positively influenced probability of mortality when controlling for age in our study. Additionally, body size has

been found to be important in the establishment of dominance hierarchies in white-tailed deer (Townsend and Bailey 1981) and other cervids (Clutton-Brock et al. 1982; Espmark 1964; Suttie 1979). We expected body size to be positively associated with probability of mortality because previous work suggests that large, dominant males exhibit more effort towards breeding activity than smaller subordinates (Miller et al. 1987). However, it is possible that body size may be a phenotypic expression of genetic quality, and large males within an age class may have a greater capacity to cope with rut-induced stresses because of superior genetics.

Unlike many populations of free-ranging cervids, deer in our study were not exposed to predation levels that may be experienced in the presence of large predators. Although coyotes (*Canis latrans*) and bobcats (*Felis rufus*), the only predators of deer at McAAP, can occasionally capture healthy adults, most of their predation is upon fawns (Caire et al. 1989; Litvaitis and Shaw 1980). As a result, their impact on the survival rates of adult, male deer is negligible, which is illustrated by low annual mortality (0.02) due to predation in our study. In contrast, Nelson and Mech (1986) found that annual mortality rates due to wolf (*Canis lupus*) predation approached 0.20 for adults. Deer populations that are exposed to large predators such as wolves or puma (*Felis concolor*) can be strongly influenced by predation and may demonstrate differences in age-specific mortality rates during adulthood that support mate competition theory. Previous studies have observed that mature deer are more vulnerable to predation by wolves (Fritts and Mech 1981; Nelson and Mech 1981), possibly because of diminished energy reserves from breeding and responsibilities of elevated social rank (Nelson and Mech 1986).

We found that young, male white-tailed deer from a population with a large proportion of mature males had patterns of mortality that differed from mature males. Young males (<3.5 years old) were more susceptible to human-induced than natural mortality agents, while older males (≥ 3.5 years old) were more likely to succumb to natural mortality agents than young males. The increase in mortality due to natural factors that we found among older age classes is consistent with mate competition theory. Young males in a population that contains a substantial proportion of mature males may not fully participate in the rut and thus may not be as susceptible to natural mortality agents that plague older deer following the breeding season.

Literature Cited

- ALLISON, P. D. 1995. Survival analysis using the SAS[®] system: a practical guide. SAS Institute Inc, Cary, North Carolina.
- BYERS, J. A. 1997. American pronghorn: social adaptations and ghosts of predators past. The University of Chicago Press, Chicago, Illinois.
- CAIRE, W., J. D. TYLER, B. P. GLASS, AND M. A. MARTES. 1989. Mammals of Oklahoma. University of Oklahoma Press, Norman, Oklahoma.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. The University of Chicago Press, Chicago, Illinois.
- COX, D. R. 1972. Regression models and life tables. Journal of the Royal Statistical Society B34:187-220.
- DASMANN, R. F., AND R. D. TABER. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143-164.

- DAVIDSON, W. R. (ED.). 1981. Diseases and parasites of white-tailed deer. Miscellaneous Publication Number 7 of the Tall Timbers Research Station, Tallahassee, Florida.
- DITCHKOFF, S. S., E. R. WELCH, JR., AND R. L. LOCHMILLER. 2000. Using cast antler characteristics to profile quality of white-tailed deer *Odocoileus virginianus* populations. *Wildlife Biology* 6:23-28.
- DITCHKOFF, S. S., E. R. WELCH, JR., R. L. LOCHMILLER, R. E. MASTERS, W. C. DINKINES, AND W. R. STARRY. 1996. Deer harvest characteristics during compound and traditional archery hunts. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 50:391-396.
- DITCHKOFF, S. S., E. R. WELCH, JR., W. R. STARRY, W. C. DINKINES, R. E. MASTERS, AND R. L. LOCHMILLER. 1997. Quality deer management at the McAlester Army Ammunition Plant: a unique approach. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 51:389-399.
- ESPMARK, Y. 1964. Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). *Animal Behavior* 12:420-425.
- FRITTS, S. H., AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs* 80:1-79.
- GEIST, V. 1971. Mountain sheep: a study in behavior and evolution. The University of Chicago Press, Chicago, Illinois.

- HARMEL, D. E. 1983. Effects of genetics on antler quality and body size in white-tailed deer. Pp. 339-353 in Antler development in Cervidae (R. D. Brown, ed.). Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.
- HEISEY, D. M. 1985. Micromort user's guide. NH Analytical Software, St. Paul, Minnesota.
- HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *The Journal of Wildlife Management* 49:668-674.
- HOLZENBEIN, S., AND R. L. MARCHINTON. 1992. Emigration and mortality in orphaned male white-tailed deer. *The Journal of Wildlife Management* 56:147-153.
- KIE, J. G., AND M. WHITE. 1985. Population dynamics of white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge, Texas. *Southwestern Naturalist* 30:105-118.
- KLEIN, D. R., AND S. T. OLSON. 1960. Natural mortality patterns of deer in southeast Alaska. *The Journal of Wildlife Management* 24:80-88.
- LITVAITIS, J. A., AND J. H. SHAW. 1980. Coyote movements, habitat use, and food habits in southwestern Oklahoma. *The Journal of Wildlife Management* 44:62-68.
- MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. The University of Michigan Press, Ann Arbor, Michigan.
- MILLER, K. V., R. L. MARCHINTON, K. J. FORAND, AND K. L. JOHANSEN. 1987. Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *Journal of Mammalogy* 68:812-817.

- MILLER, K. V., R. L. MARCHINTON, AND J. J. OZOGA. 1995. Deer sociobiology. Pp. 118-128 in *Quality whitetails: the how and why of quality deer management*. (K. V. Miller, and R. L. Marchinton, eds.). Stackpole Books, Mechanicsburg, Pennsylvania.
- MILLER, K. V., AND R. L. MARCHINTON, (EDS.). 1995. *Quality whitetails: the why and how of quality deer management*. Stackpole Books, Mechanicsburg, Pennsylvania.
- NELSON, M. E., AND L. D. MECH. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs* 77:1-53.
- NELSON, M. E., AND L. D. MECH. 1986. Mortality of white-tailed deer in northeastern Minnesota. *The Journal of Wildlife Management* 50:691-698.
- NESBITT, W. H. AND P. L. WRIGHT, (EDS.). 1981. *Records of North American big game*. The Boone and Crockett Club, Alexandria, Virginia.
- OWEN-SMITH, N. 1993. Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *Journal of Animal Ecology* 62:428-440.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. *The Journal of Wildlife Management* 53:7-15.
- RAMSEY, C. W. 1968. A drop-net deer trap. *The Journal of Wildlife Management* 32:187-190.
- ROBINETTE, W. L., J. S. GASHWILER, J. B. LOW, AND D. A. JONES. 1957. Differential mortality by sex and age among mule deer. *The Journal of Wildlife Management* 21:1-16.

- ROSEBERRY, J. L., AND W. D. KLIMSTRA. 1974. Differential vulnerability during a controlled harvest. *The Journal of Wildlife Management* 38:499-507.
- SAS INSTITUTE INC. 1988. SAS/STAT user's guide; release 6.03. Statistics. SAS Institute Inc., Cary, North Carolina.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *The Journal of Wildlife Management* 13:195-226.
- SUTTIE, J. M. 1979. The effect of antler removal on dominance and fighting behaviour in farmed red deer stags. *Journal of Zoology* 190:217-224.
- TOWNSEND, T. W., AND E. D. BAILEY. 1981. Effects of age, sex and weight on social rank in penned white-tailed deer. *American Midland Naturalist* 106:92-101.

Table 1. Estimated annual probability of mortality (P_m) from various causes for adult, male white-tailed deer in a population from southeastern Oklahoma.

Cause of death	n	P_m	SE	95% C.I.	
				Lower	Upper
Hunting	18	0.124	0.027	0.071	0.178
Vehicle collisions	3	0.021	0.012	0.000	0.044
Poaching	3	0.021	0.012	0.000	0.044
Predation	3	0.021	0.012	0.000	0.044
Other ^a	4	0.028	0.014	0.001	0.055
Unknown	8	0.055	0.019	0.018	0.093

^a Causes of mortality that were classified as 'Other' were a leg infection, thoracic puncture during a fight, brain abscess, and exhaustion from breeding activity.

Table 2. Estimated annual probability of mortality (P_m) due to natural or human-induced factors for adult, male white-tailed deer 1.5-2.5, 3.5-4.5, and ≥ 5.5 years old in a population from southeastern Oklahoma.

Mortality agent	n	P_m	SE	95% C.I.	
				Lower	Upper
1.5-2.5 years old					
Human-induced	5	0.133	0.055	0.024	0.241
Natural	1	0.027	0.026	0.000	0.078
3.5-4.5 years old					
Human-induced	13	0.209	0.051	0.108	0.310
Natural	8	0.129	0.042	0.046	0.212
≥ 5.5 years old					
Human-induced	6	0.133	0.050	0.034	0.231
Natural	6	0.133	0.050	0.034	0.231

Table 3. Estimated risk ratios of morphological and physiological parameters for overall and human-induced mortality hazards in white-tailed deer from southeastern Oklahoma.

Variable	All mortality					Human-induced mortality				
	Parameter				Risk	Parameter				Risk
	estimate	SE	X^2	<i>P</i>	ratio ^a	estimate	SE	X^2	<i>P</i>	ratio
Age	-1.0215	0.3962	6.7	0.001	0.360	-3.8511	0.9163	17.7	0.001	0.021
Body length	0.0441	0.0406	1.2	0.277	1.045	0.0840	0.0525	2.6	0.109	1.088
Chest girth	0.0008	0.0057	0.0	0.892	1.001	0.0043	0.0076	0.3	0.575	1.004
Antler score	0.0240	0.0111	4.7	0.030	1.024	0.0994	0.0258	14.8	0.001	1.105
Ticks	0.1117	0.0562	4.0	0.047	1.118	0.2742	0.1062	6.7	0.010	1.315
Leukocytes	-0.0013	0.0120	0.0	0.912	0.999	-0.0005	0.0205	0.0	0.979	0.999
BUN	0.0502	0.0380	1.7	0.187	1.051	0.1199	0.0619	3.8	0.053	1.127
Total protein	-0.0304	0.0760	0.2	0.689	0.970	-0.0018	0.0957	0.0	0.985	0.998
Albumin	-0.0697	0.2157	0.1	0.746	0.933	0.1470	0.2140	0.5	0.492	1.158
CPK	0.0031	0.0017	3.4	0.065	1.003	0.0097	0.0044	4.9	0.027	1.010

^a Risk ratio is the predicted change in the probability of mortality due to a 1-unit increment increase in the variable of interest. A risk ratio <1.0 indicates that probability of mortality would decrease and a risk ratio >1.0 indicates that probability of mortality would increase.

Figure 1. Annual probability of survival of adult, male white-tailed deer in a population from southeastern Oklahoma. Survival curves were calculated using the Kaplan-Meier method.

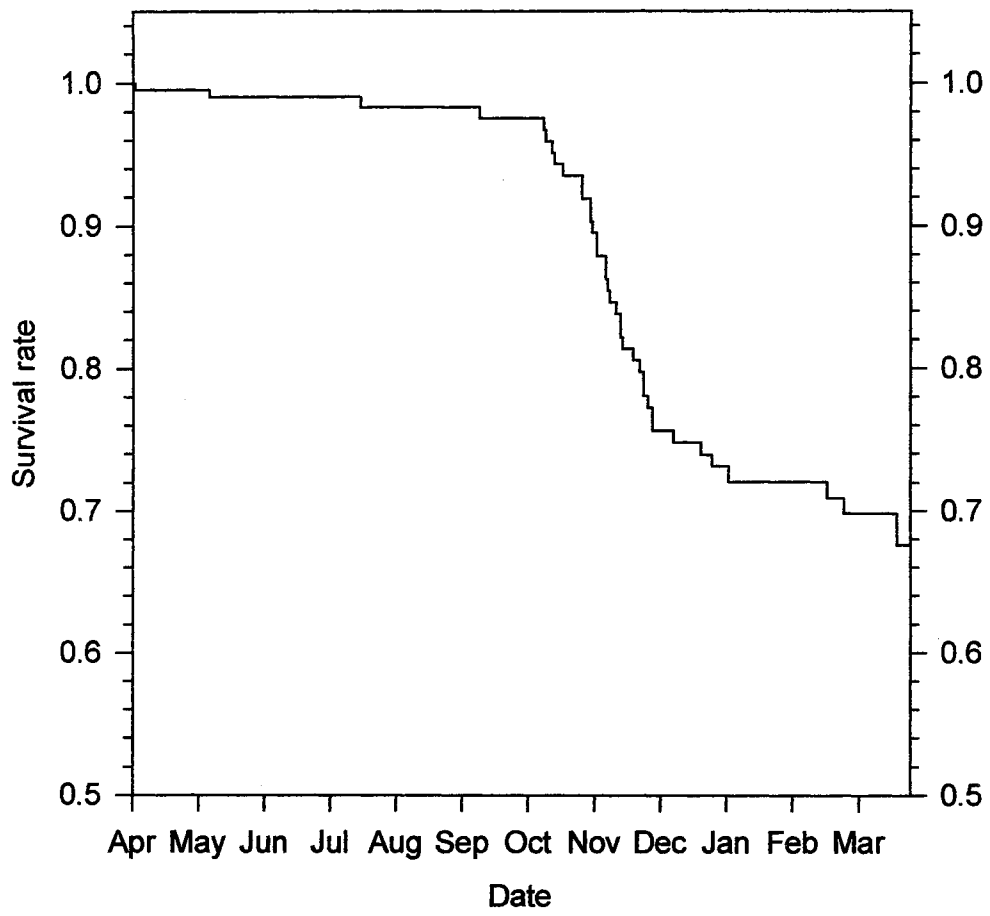
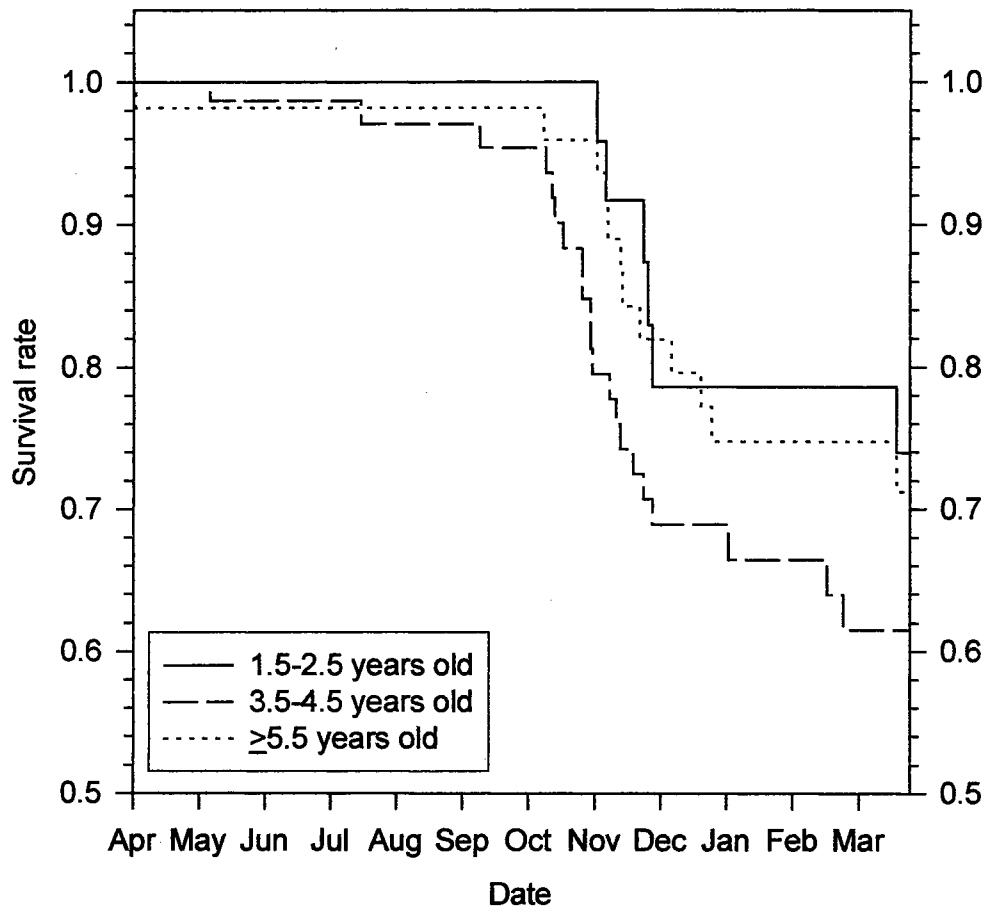


Figure 2. Annual probability of survival of adult, male white-tailed deer in a population from southeastern Oklahoma that were 1.5-2.5, 3.5-4.5, and ≥ 5.5 years old. Survival curves were calculated using the Kaplan-Meier method.



VITA

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Doctor of Philosophy

**Thesis: HONEST ADVERTISEMENT IN MALE WHITE-TAILED DEER:
EVIDENCE FOR THE HANDICAP HYPOTHESIS OF MATE SELECTION**

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