Does fluctuating asymmetry of antlers in white-tailed deer (*Odocoileus virginianus*) follow patterns predicted for sexually selected traits?

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Secondary sexual characters have been hypothesized to signal male quality and should demonstrate a negative relationship between the size of the trait and degree of fluctuating asymmetry because they are costly to produce. We collected morphometric and antler data from 439 white-tailed deer (*Odocoileus virginianus*) in Oklahoma, USA, in order to determine whether measures of antler asymmetry follow the patterns predicted for sexually selected characters. Relative fluctuating asymmetry was negatively related to antler size for all deer and within age groups up to five and a half years of age. We did not detect an association between asymmetry and antler size among deer that were six and a half years or older. When categorizing deer by antler size, we found that deer with small antlers ($\leqslant$33rd percentile) had greater levels of relative asymmetry than deer with large antlers ($\leqslant$67th percentile). The relative asymmetry of antlers was negatively related to age and was greatest in deer that were one and a half years old. Relative asymmetry was also negatively related to carcass mass, inside spread, skull length and body length. These data suggest that asymmetry in the antlers of white-tailed deer may be a reliable signal of quality and, as such, may be important in maintaining honesty in intrasexual advertisements during the breeding season.

Keywords: antlers; fluctuating asymmetry; handicap hypothesis; *Odocoileus virginianus*; sexual selection; white-tailed deer

1. INTRODUCTION

Fluctuating asymmetry is a measure of deviation from perfect bilateral symmetry in the development of morphologic characters that would normally be symmetrical (Van Valen 1962) and results from an individual's inability to cope with environmental stresses (parasites, disease, nutrition, climate, pollution, etc.) or physical damage (Baccus & Welch 1982) adequately during the development of characters that are normally symmetrical (Nilsson 1994). Fluctuating asymmetry increases as the developmental ability of an individual is increasingly impaired by environmental stresses. As a result, fluctuating asymmetry might serve as an indicator of the level of stress experienced by an individual (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). Individuals with a greater capacity to cope with stress (i.e. high-quality individuals) are predicted to have lower levels of asymmetry relative to other individuals in a population.

Because of the implications that asymmetry could serve as a signal of quality between sexes during mate selection (Møller 1993), most research on fluctuating asymmetry has focused on sexually selected traits (see Møller & Swaddle 1997). Sexually selected traits are morphological

characters that can generally be classified into two categories (Møller 1992): elaborate secondary sexual characters (e.g. ornate feathers and bright colours) that serve primarily as an advertisement to the opposite sex and structures used during intrasexual combat (e.g. antlers, horns and spurs). Cervid antlers are generally included in the second category and many published accounts have described intrasexual combat among cervids (see Geist 1981, 1982; Clutton-Brock *et al.* 1982; Goss 1983; Marchinton & Hirth 1984). Even the huge palmated antlers of the extinct Irish elk (*Megaloceros giganteus*), which have been proposed to be structures for advertisement (Gould 1974), have structural properties required to withstand mechanical stresses imposed by intrasexual combat (Kitchener *et al.* 1994). In addition to their function in combat, cervid antlers probably serve as signals of quality to potential competitors during the breeding season (Gould 1974), as do horns in mountain sheep (*Ovis canadensis*) (Geist 1966). Because of the potential for fluctuating asymmetry to signal quality and capacity to cope with environmental stress, the fluctuating asymmetry of cervid antlers could be a reliable index of the quality of a male cervid during intrasexual advertisement.

Møller (1992) proposed that the fluctuating asymmetry of morphological characters that serve as weapons exhibits a negative association between size of the weapon and degree of asymmetry, which is the same pattern that has been described for sexually selected traits that have evolved solely for display (Møller 1993). Because

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secondary sexual characters are costly to produce, individuals that produce the greatest ornamentation (i.e. greater allocation of resources) should represent high-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 1992, 1993). Solberg & Sæther (1993) further predicted that there should be an inverse relationship between the degree of 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 and resource acquisition) of the cohort as inferior animals are selected against.

White-tailed deer (*Odocoileus virginianus*) are a good cervid model for testing the predictions of Møller (1992) because their level of sociality lies near the centre of a continuum of cervids ranging from solitary species such as the pudu (*Pudu puda*) to highly social species such as caribou (*Rangifer tarandus*). Unlike solitary cervids with short, simple antlers that are used primarily as weapons in territorial defence (Putman 1988), antler structure in white-tailed deer is more complex, suggesting that antlers in this species could be important during display. However, the antlers of white-tailed deer are not as complex as the palmated antlers of caribou or red deer (*Cervidus elaphus*) with their intricate branching. These species tend to be highly social where display is probably more important than in white-tailed deer (Clutton-Brock *et al*. 1982).

We gathered antler and morphometric data from hunter-harvested, male white-tailed deer in order to determine whether antler asymmetry may be an index of quality. Specifically, we tested the predictions of Møller (1992) and Solberg & Sæther (1993) and determined whether antler asymmetry was negatively related to antler size and age. We hypothesized a negative association between antler size and asymmetry because the structure of white-tailed deer antlers suggests a display function. In addition, if asymmetry of white-tailed deer antlers does signal quality, then we would expect the average quality of a cohort to increase with time and there to be a negative association between age and antler asymmetry.

2. MATERIAL AND METHODS

Our study population consisted of white-tailed deer harvested by hunters or captured by drop-net at the McAlester Army Ammunition Plant in south-eastern Oklahoma, USA (34°49′ N, 95°55′ W). The McAlester Army Ammunition Plant is an 18 212 ha area owned and operated by the US Department of Defense and has been managed in order to maintain a large proportion ($\geq 55\%$) (Ditchkoff *et al*. 2000) of mature males in the population (i.e. quality deer management) since 1989 (Ditchkoff *et al*. 1997). An annual census indicated that herd density (12–13 deer km^{-2}) was below carrying capacity and that the buck-to-doe ratio was 1:2.2. The McAlester Army Ammunition Plant has limited public access and is open to traditional archery hunting via a lottery (drawing). Approximately 1500 hunters participate in the hunts annually and have an average

success rate of 10.7% (Ditchkoff *et al*. 1996, 1997). The predominant vegetation types at the McAlester Army Ammunition Plant are meadows of native prairie grass (*Andropogon virginicus*, *Andropogon gerardii* and *Schizachyrium scoparium*) bisected by brushy draws (*Ulmus alata*, *Symphoricarpos orbiculatus*, *Prunus angustifolia* and *Diospyros virginiana*), oak (*Quercus nigra* and *Quercus shumardii*) bottomlands and post oak (*Quercus stellata*)–blackjack oak (*Quercus marilandica*) uplands.

We collected data from hunter-harvested deer during 1994–1996 and 1999 ($n = 359$) and deer captured using drop-nets from December to January during 1994–1995, 1995–1996 and 1996–1997 ($n = 80$). Captured deer were measured and released after affixing a radiocollar for further study. Antlers were measured according to the Boone and Crockett scoring system described by Nesbitt & Wright (1981) in order to obtain an estimate of total antler development. The Boone and Crockett scoring system 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 the 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 four circumferences for each antler). This scoring system also penalizes for asymmetry of antlers, but we did not include asymmetry deductions in our measurements of antlers, resulting in separable scores for the right and left antlers and a total gross score that included scores from both antlers and measurement of inside spread. We did not include scores for animals that had broken tines or main beams in the analysis. We did not measure the lengths of all tines during 1994 so we could not calculate antler scores for 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 and relative asymmetry was calculated as absolute asymmetry divided by the larger antler. Relative asymmetry measurements adjusted absolute asymmetry measurements for 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. Measurements of absolute and relative fluctuating asymmetry were calculated for antler score, number of points, main beam length and basal circumference. In order to assess how measurement error affected asymmetry calculations, we made duplicate measurements on 11 sets of antlers and calculated errors for measurement of beam circumferences, tine lengths, main beam length, antler score and inside spread.

We used Pearson correlations for examining relationships between the asymmetry measurements of antler score, number of points, main beam length and basal circumference. We compared the variability of relative symmetry within age classes using Levene's test. We arcsine transformed relative fluctuating asymmetry data before all parametric tests (Zar 1984). We tested for year and age effects on relative and absolute asymmetry using two-way analysis of variance (ANOVA). We used weighted regression with inverse variance as the weight for assessing relationships between asymmetry and age. We used simple linear regression for assessing relationships between asymmetry (absolute and relative) and the score of the larger antler rather than the total or mean score of both antlers (Sullivan *et al*. 1993). We
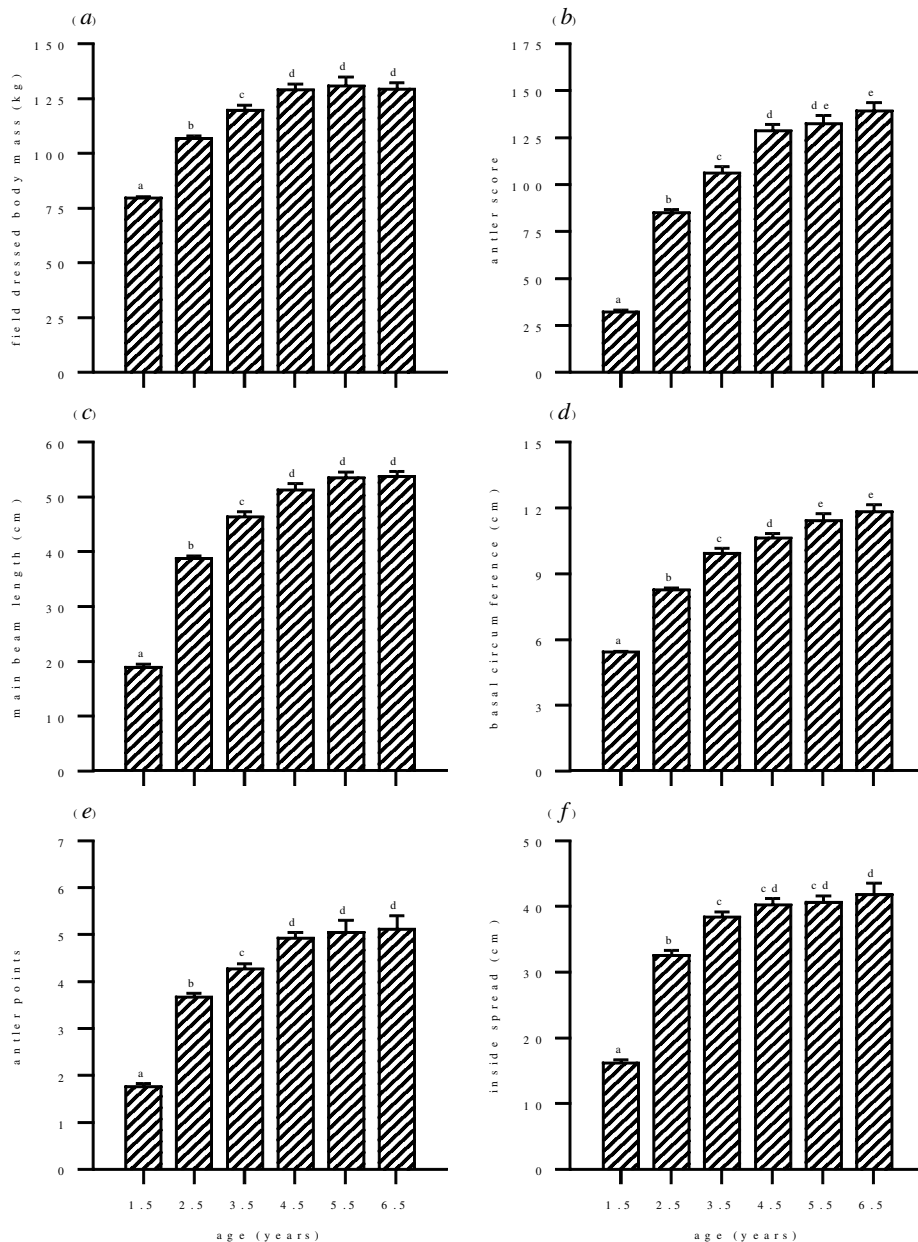
Figure 1. Age-specific differences in mean (± s.e.) (*a*) body mass, (*b*) antler score, (*c*) main beam length, (*d*) basal circumference, (*e*) number of antler points and (*f*) inside spread of white-tailed deer from a population in south-eastern Oklahoma. Means with different letters differ ($p \leqslant 0.05$) based upon least-square means analysis.

also used simple linear regression for determining relationships between asymmetry (absolute and relative) and the gross Boone and Crockett score. We tested for relationships between morphometric measurements and relative asymmetry using Spearman's rank correlations (r_S). Individuals of six and a half years of age or older were grouped for age analyses because of difficulty in ageing older animals (Jacobson & Reiner 1989), because antlers approach their greatest size between six and a half and seven and a half years of age in white-tailed deer (Cook 1984) and because males of six and a half years of age or older represent a relatively small proportion (3.6%) of the population sample. We compared the degree of relative asymmetry among groups of deer with low, medium and high levels of antler development using ANOVA. We classified deer into low ($\leqslant$ 33rd percentile), medium (33rd–66th percentile) and high ($\geqslant$ 67th percentile) groups based on antler score within each age class and then

combined deer across ages in order to allow analysis without the confounding effects of age (R. T. Bowyer, personal communication). All analyses were performed with the Statistical Analysis System (SAS Institute, Inc. 1990).

3. RESULTS

The antler sets used to determine measurement error had antler scores ranging from 55.875 to 166.625 points. The mean measurement errors for beam circumference, antler point and main beam measurements were 1.23 mm ($n = 80$ and s.e. $= 0.22$), 2.13 mm ($n = 61$ and s.e. $= 0.56$) and 6.06 mm ($n = 22$ and s.e. $= 1.10$), respectively. The mean measurement error for absolute asymmetry of antler score was 10.24 mm ($n = 22$ and s.e. $= 1.96$) or 0.40 points ($n = 22$ and s.e. $= 0.08$), which equates to 0.99%

Table 1. *Correlation matrix reflecting relationships between measures of relative fluctuating asymmetry for antlers of white-tailed deer in south-eastern Oklahoma, 1994–1996*

character	score	beam length	basal circumference	antler points
score				
r	1.000	—	—	—
p	0.000	—	—	—
n	296	—	—	—
beam length				
r	0.760	1.000	—	—
p	0.001	0.000	—	—
n	296	376	—	—
basal circumference				
r	0.501	0.405	1.000	—
p	0.001	0.001	0.000	—
n	296	376	391	—
antler points				
r	0.415	0.092	0.161	1.000
p	0.001	0.077	0.002	0.000
n	296	373	378	381

($n = 22$ and s.e. $= 0.16$) error for relative asymmetry of antler score. Because the error was less than 1% we did not adjust our data prior to analysis.

Carcass mass, gross Boone and Crockett score, main beam length, basal circumference, number of antler points and inside spread increased with age ($p < 0.001$) (figure 1). The mean asymmetry for the sampled population did not differ from zero ($p = 0.136$), indicating that there was no directional asymmetry. Because measurements of asymmetry in antler score were positively correlated with all other asymmetry measurements ($0.41 \leqslant r \leqslant 0.76$ and $p \leqslant 0.001$) (table 1) and antler score was the best index of overall antler size (Marchinton *et al.* 1995), all references to asymmetry measurements, unless otherwise stated, are for antler score. Relative asymmetry was negatively associated with body mass ($r_S = -0.38$ and $p < 0.001$), inside spread (greatest distance between the main beams) ($r_S = -0.46$ and $p < 0.001$) and body length ($r_S = -0.31$ and $p < 0.001$). These relationships did not hold true ($p > 0.05$) within age classes with the exception of one-and-a-half-year-old inside antler spread ($r_S = -0.33$ and $p < 0.001$).

We found no difference in the magnitude of relative asymmetry in deer antlers between years ($p = 0.999$), but observed that one-and-a-half-year-olds had greater ($p \leqslant 0.001$) relative asymmetry than other age classes (figure 2). There was a negative relationship between relative asymmetry and age (relative asymmetry $= 0.064 + 0.279(1/\text{age}^2)$) ($r^2 = 0.13$ and $p < 0.001$). In contrast, we found a weak, positive association between age and absolute asymmetry of antler score (absolute asymmetry $= 2.101 + 0.435(\text{age})$) ($r^2 = 0.03$ and $p = 0.002$) and one-and-a-half-year-old deer had lower ($p < 0.05$) levels of absolute asymmetry than deer that were three and a half, five and a half and six and a half years or older. Relative asymmetry was negatively related to antler score (relative asymmetry $= 0.241 - 0.002(\text{score})$) ($r^2 = 0.21$ and $p < 0.001$) (figure 3). That relationship was also negative for deer aged one and a half ($r^2 = 0.14$ and $p < 0.001$), two and a half ($r^2 = 0.19$ and $p < 0.001$), three and a half ($r^2 = 0.27$ and $p < 0.001$) and five and a half

years old ($r^2 = 0.32$ and $p = 0.037$). However, associations between size and relative asymmetry of antler score tended to be negative but non-significant among four-and-a-half-year-old deer ($r^2 = 0.12$ and $p = 0.072$) and there was no relationship among deer that were six and a half years or older ($r^2 = 0.05$ and $p = 0.404$). There was a weak, positive relationship (absolute asymmetry $= 2.486 - 0.010(\text{score})$) ($r^2 = 0.01$ and $p = 0.051$) between absolute asymmetry and size (antler score) of antlers. The relative asymmetry of antler score, main beam length and basal circumference was greater ($p < 0.05$) among small-antlered deer than medium- or large-antlered deer, but the relative asymmetry of the number of antler points did not differ ($p > 0.25$) between groups (figure 4).

4. DISCUSSION

The relative asymmetry of antler score in white-tailed deer followed the pattern predicted for a secondary sexual trait that is used as a weapon (Møller 1992); as antler size increased, relative fluctuating asymmetry decreased. This pattern suggests that males with larger antlers are able to cope with environmental stresses during development better than their counterparts with smaller antlers, and that fluctuating asymmetry in antlers may serve as an index of quality. 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 then follows that individuals with large antlers should have the least stress-induced asymmetry if they are the highest quality deer (Møller 1992) and it is plausible that asymmetry in antlers could thereby signal quality to competitors during the breeding season. A negative relationship between antler size and degree of asymmetry has been reported for reindeer (Markusson & Folstad 1997) and roe deer (*Capreolus capreolus*) (Pelabon & Van Breukelen 1998). In both cases, the authors suggested that asymmetry of antlers signalled male quality. In contrast, Solberg & Sæther (1993) did not find a negative relationship between asymmetry and antler size in moose (*Alces alces*), which may have been an artefact of correlating the
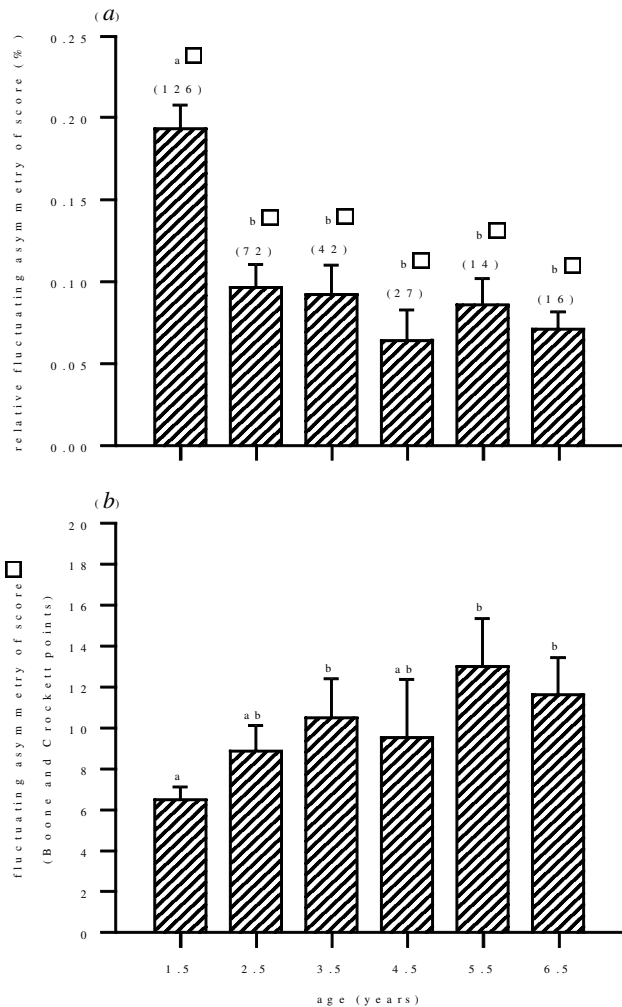
Figure 2. Age-specific changes in mean (± s.e.) measures of absolute and relative asymmetry of antler score in white-tailed deer from a population in south-eastern Oklahoma. Means with different letters differ ($p \leqslant 0.05$) based upon least-square means analysis. Numbers in parentheses are sample sizes (n) for each group.
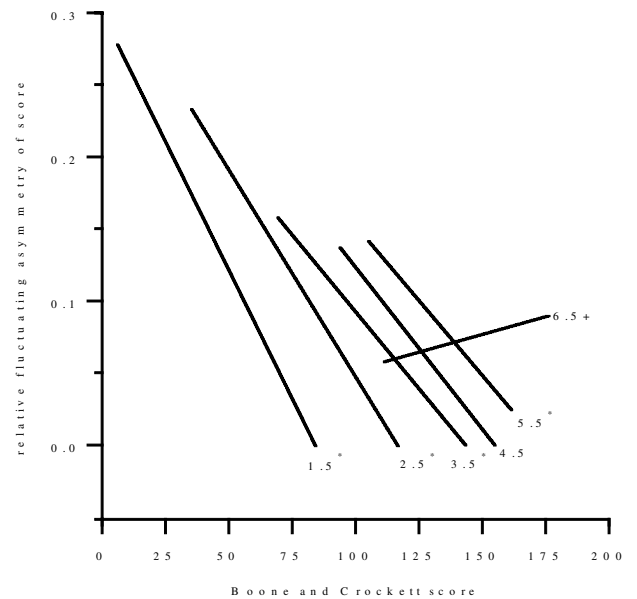

Figure 3. Regression relationships between antler score and relative asymmetry of score for six age classes of white-tailed deer from a population in south-eastern Oklahoma. Regression lines are labelled with age class (years) and asterisks indicate regression lines that were significant ($p < 0.05$).

number of antler points with degree of asymmetry. It is possible that a different index to antler size (e.g. antler length, spread or Boone and Crockett score) (Nesbitt & Wright 1981) would be more appropriate in a species with a high degree of antler palmation.

We hypothesize that, if fluctuating asymmetry of antlers is a measure of quality in white-tailed deer, it should be correlated with some index of animal condition. For example, the number of visible ribs has been positively correlated with horn asymmetry in gemsbok (*Oryx gazella*) (Møller *et al.* 1996). Body mass is a good measure of condition because it ultimately represents 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 the quality of an individual. Similarly, Solberg & Sæther (1993) reported a negative relationship between body size and asymmetry in moose.

In contrast to the overall pattern of decreasing relative asymmetry with antler size, deer of six and a half years or older had no relationship between relative asymmetry and antler size, although the sample size in our study was relatively small ($n = 16$). If antlers are to be an honest signal, then there must be a cost (Ullrey 1983; Folstad *et al.* 1989) associated with their production (Zahavi & Zahavi 1997). Secondary sexual characters should, through sexual selection, increase in size to some threshold where the benefits of the character are balanced by the costs of production (Fisher 1930). Antlers in white-tailed deer of six and a half years or older 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 white-tailed deer of six and a half years or older may be approaching the upper threshold of production based upon the nutrient requirements in our study area. Although the relative asymmetry of antlers of deer of six and a half years or older was not greater than in other age classes, the lack of a 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, possibly representing a final effort at reproduction because of approaching senescence. Nilsson (1994) reported that asymmetry can be influenced by the rate at which nutrients are secured by an individual, and Baccus & Welch (1982) and Pelabon & Van Breukelen (1998) reported elevated asymmetry in the antlers of sika (*Cervus nippon*) 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 of six and a
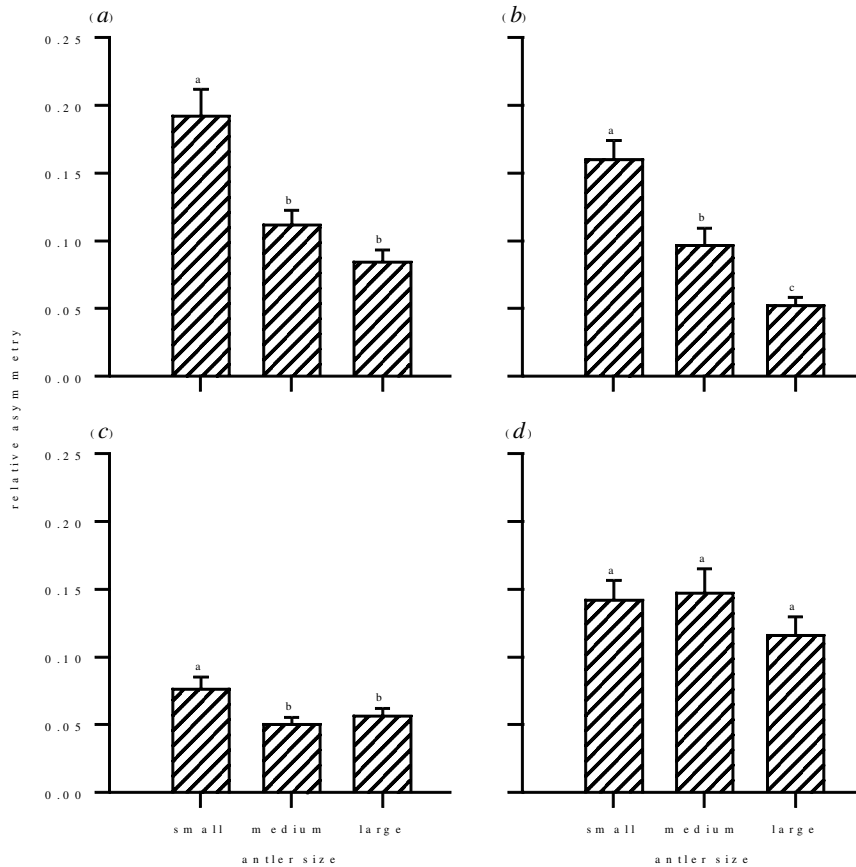
Figure 4. Relative asymmetry (as a percentage) of (*a*) antler score, (*b*) main beam length, (*c*) basal circumference and (*d*) number of antler points of white-tailed deer with small, medium and large antlers relative to age. Bars labelled with different letters differ ($p \leqslant 0.05$) based upon least-square means analysis.

half years or older in our study area, we would expect no 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 the quality of an individual or its ability to cope with environmental stresses, we would expect that low-quality individuals (high asymmetry) would have a 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 in a cohort should decrease as it ages, creating a negative relationship between asymmetry and age. Our prediction that variability in asymmetry within a cohort should decrease as a cohort ages was also 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 to 30% (Gavin *et al.* 1984; Nelson & Mech 1986; DeYoung 1989). Estimates in our population suggested that natural mortality agents account for *ca.* 40% of the mortality among adult males (Ditchkoff *et al.* 2001). As a result, there is a propensity for natural selection to modify the 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.

An alternative hypothesis for explaining the negative relationship we found between antler size and asymmetry is that those deer with low levels of asymmetry are in good condition because they do not participate in rutting activities. Geist (2000) proposed that deer with the largest antlers often do not participate in the rut and, thus, do not experience the rigours associated with breeding activities, such as nutritional stress or wounding (Geist 1986). Under this scenario, males with low levels of antler asymmetry would not necessarily be high-quality males but beneficiaries of non-stressful behaviour. We cannot discount the possibility that this does not occur in some cases. However, based upon visual observations and telemetry data (S. S. Ditchkoff, unpublished data), we contend that massive-antlered deer do participate in breeding activities in our study area. Similarly, others have found that large-antlered males do most of the breeding among cervids (Hirth 1977; Clutton-Brock *et al.* 1982; Bowyer 1986; Van Ballenberghe & Miquelle 1993; Weckerly 1998). If non-participants in the rut are present in the population we studied, we contend that they are a negligible component of the population.

Our measurements of relative asymmetry in white-tailed deer followed the pattern predicted by Møller (1992), whereas those of absolute asymmetry did not. As a

character increases in size, its potential for absolute deviation from perfect bilateral symmetry should also increase. Baccus & Welch (1982) reported that age (which is representative of antler size) and absolute asymmetry of antlers were positively correlated in sika deer (*C. nippon*). Similarly, we observed increased absolute asymmetry as trait size increased in our population, although the relationship was poor. In contrast, relative asymmetry had a strong, negative relationship with size in antlers. Measurements of relative asymmetry correct absolute asymmetry for biases caused by trait size 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 measurements 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 more than nine times larger (Ditchkoff *et al.* 2000) in mature than immature deer. These characteristics suggest that the 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 the antlers of a mature deer cannot be directly compared to a 10 cm difference in the spikes of a young buck unless relative asymmetry is used. In actuality, 10 cm of variation between 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 the spikes of a young male.

The fluctuating asymmetry of antlers in white-tailed deer followed the patterns predicted for a sexually selected trait that is used as a weapon (Møller 1992) and may help signal the quality of a deer to competitors during intrasexual advertisements in the breeding season. These data have important implications for theories of how dominance hierarchies are established among cervids. We did not actually test whether asymmetry is used as a measure of quality during intrasexual advertisements, but our results suggest that further studies are needed in order to assess what antler characteristics are important during display.

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