Antler Breakage Patterns in White-tailed Deer

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Abstract: Antlers contribute greatly to the life history and ecology of most species in the deer family (Cervidae). Diet composition and quality, precipitation, age, antler size, dominance rank, and demographic parameters (e.g., adult sex ratio, density) of the population may explain variation in antler breakage rates between individuals and subpopulations. Our objectives were to examine the effects of some of these variables on probability of antler breakage and provide a general description of antler breakage patterns in white-tailed deer (*Odocoileus virginianus*). From 2001–2010, we collected 487 shed antlers from captive white-tailed deer managed at relatively high densities with a sex ratio skewed towards males. Overall antler breakage rate was 30% with approximately 51% of antlered males possessing ≥1 broken antler (at least one antler point or the main beam broken). Beam circumference ($\beta = -0.016$) and total number of antler points ($\beta = 0.169$) had the greatest effect on probability of antler breakage. The main beam and G2 antler point were least susceptible to breakage. No effect of seasonal precipitation was documented, but supplemental feed was available ad libitum possibly alleviating nutritional stress due to drought and reducing the effect of precipitation levels on antler breakage. The study provides a general description of antler breakage in a white-tailed deer herd and reaffirms that antler breakage is likely a byproduct of many interwoven individual antler, herd demographic, and environmental variables. From statewide agencies to individual properties, managers should consider how antler breakage patterns may affect harvest regulations based on antler characteristics and how management schemes designed to maximize trophy antler potential may be impacted.

Key words: antler breakage, Cervidae, *Odocoileus virginianus*, white-tailed deer

The ecology and behavior of white-tailed deer (*Odocoileus virginianus*) and most other cervids are inextricably linked to the family's most notable secondary sexual characteristic—antlers (Geist 1966). In a polygynous mating system, males must aggressively contend for females during the breeding season, and antler and body size are usually correlated with dominance (Geist 1966, Clutton-Brock 1987). Because antlers are used for intrasexual combat, the largest antlered individuals are often most successful in competition and may sire more offspring (Kruuk et al. 2002). Cervid antlers follow an annual cycle of growth, mineralization, and shedding with subsequent sets of antlers progressing in both mass and dimension. Mature males usually have larger antlers than younger animals, though antler size may decrease in post-mature, senescent individuals (Anderson and Medin 1969, Scribner et al. 1989, Stewart et al. 2000, Vanpe et al. 2007). Antler symmetry may convey individual genetic quality (Moller and Pomiankowski 1993, Ditchkoff et al. 2001); however, pedicle, antler, and body injuries may adversely affect antler development (Marburger et al. 1972, Hicks and Rachlow 2006). Antler breakage or malformation, whether it occurs in the growth (velvet) or mineralized (after velvet shedding) stages, could reduce a male's ability to compete and breed successfully (Espmark 1964, Lincoln 1972).

Though researchers have studied antlers in terms of their morphometry (McCullough 1982), composition (Miller et al. 1985, McDonald et al. 2005), density (Miller et al. 1985), break strength (McDonald et al. 2005, Landete-Castillejos et al. 2010), and growth processes (French et al. 1956, Scribner et al. 1989), no studies have examined patterns or rates of breakage in white-tailed deer antlers—an aspect of antler biology that potentially affects white-tailed deer management/harvest regulations and the evolutionary role of mate selection through quality advertisement (fluctuating asymmetry; Ditchkoff et al. 2001). McDonald et al. (2005) found that increased rainfall may affect the mineral composition of shed antlers and increase the force required to break antlers. Cowan and Long (1962) noted that antlers attain normal development when adequate rainfall produces plentiful summer forage. It is believed the ratio of spongy bone (spongiosa) to hard sheath greatly influences the propensity of antlers to break (Chapman 1980). Increasing the percentage of spongiosa enhances an antler's capacity to withstand the impact forces experienced during fights between male competitors (Chapman 1980). Miller et al. (1985) noted that the proportion of spongiosa increased in antlers with greater mass, and it was hypothesized that younger deer with smaller antlers should experience higher rates of antler breakage

from a purely physical standpoint (a pattern followed by red deer [*Cervus elaphus*]; Lincoln 1972). The most mineralized portions of an antler (i.e., tines closest to the antler base and distal portion of individual tines) are the densest with the least spongiosa, and antlers were least dense in the portion of the main beam between the second and third tines (Miller et al. 1985).

McDonald et al. (2005) suggested that factors unrelated to the physical composition of antlers may better explain antler breakage rates within and between populations; reasons such as adult sex ratio, population density, nutritional deficiencies, and individual dominance and aggression levels were cited. Age-related differences in aggression and dominance may have an impact on the frequency of fighting among younger, smaller-antlered males versus older, larger-antlered males (Johnson et al. 2007b). Similarly, a population with an even sex ratio or high density of males may experience greater intensity of intrasexual competition and relatively greater antler breakage rates compared to a deer population with a sex ratio skewed towards females (McDonald et al. 2005). This dynamic may be exacerbated within enclosed deer populations where agonistic interactions may increase due to high mature male densities. Johnson et al. (2005, 2007b) described a population of tule elk (*Cervus elaphus nannodes*) that exhibited an antler breakage rate of 82% possibly due to nutritional deficiencies (Johnson et al. 2007a)—much greater than the proposed 5% average for members of the Cervidae family (Henshaw 1971).

Our objectives were to document the morphological patterns of antler breakage and correlate breakage to: 1) characteristics such as antler circumference and number of typical and total antler points and 2) precipitation. We hypothesized that antlers with greater basal circumference (i.e., higher spongy bone: compact bone ratio) would have greater resistance to breakage. However, we surmised that an equally plausible hypothesis was that despite possessing some antler traits resistant to breakage, large-antlered males would suffer greater breakage rates because of increased fighting bouts and having more points available to break. Also, we hypothesized that drier years would cause antler mass to be below average with less spongiosa and increase likelihood of antler breakage.

Study Site

Three Notch Wildlife Research Foundation (hereafter Three Notch) is a privately-owned property located 10 km east of Union Springs, Alabama. The study area encompasses 258.2 ha and has been enclosed by 3-m deer proof fencing since 1997. Approximately 20% of the available habitat (48 ha) is farmed to provide deer with an array of both cool-season and warm-season forages. The remainder of the habitat is a matrix of loblolly pine (*Pinus taeda*) stands and mature hardwood forest. Prescribed fire is used each year in upland areas to facilitate searches for shed antlers as well as to provide natural browse for deer. Also, supplemental protein pellets (20% protein) are available ad libitum throughout the year at permanent feeding stations distributed throughout the property (1 feeder/22 ha).

Shed antler collections began four years after the high fence was erected in 1997. The initial population structure was skewed towards females, and yearling males comprised the majority of the male segment of the population. By 2001, the sex ratio became even (1 female:1 male) through aggressive antlerless deer harvest, and the number of individual males in mature age classes increased because bucks were protected from harvest for the initial three years following fence closure. Due to limited hunting success (archery equipment only), the selective harvest of the landowner, and an abundance of food sources, the enclosure became densely populated with a sex ratio favoring males. A mark-recapture camera survey (Jacobson et al. 1997) conducted in fall 2007 produced a density estimate with a minimum of 1 deer per 1.7 ha, which is more than three times the density normally found in this region, and an adult sex ratio of 2:1 (male:female; McCoy et al. 2011).

Methods

From April 2001–June 2010, we collected shed antlers during both organized and opportunistic searches at Three Notch. We omitted antlers damaged by considerable rodent gnawing, decomposition, or accidental contact with farming equipment. By examining the weathering, color, and position of antlers in the forest duff layer, we included only antlers recovered within six months of shedding to ensure that all samples were correctly classified by year. With no way of knowing whether seemingly similar-looking right and left side antlers came from the same individual, we analyzed only left antlers to avoid pseudoreplication.

For each antler, we recorded calendar year of growth (different from year of collection), beam circumference (nearest mm), number of typical points, total number of points (included both typical and non-typical points), and whether the main beam and each point was intact or broken. All measuring was done by the same investigator to ensure consistency, and measurements were made using a 6.35 mm-wide metal measuring tape with mm markings. Beam circumference was measured at the narrowest point of the main beam between the antler base and the first typical antler point (same as H1 measurement of the Boone and Crockett measuring protocol; Ditchkoff et al. 2001). Typical antler points were those that originate upwards from the main beam and were numbered in sequence from the antler base to the end of the main beam, such that the G1 tine was the nearest antler point to the base. We considered a projection to be a point only if it measured at least

2.54 cm in length and its length exceeded its width. Non-typical points were all other antler points (e.g., points originating from an already existing antler point, points originating from the main beam but pointing in a downwards or otherwise abnormal direction). "Broken" antlers had at least one antler point or the main beam broken in a transverse manner (Jin and Shipman 2010), and "intact" antlers did not possess any breaks. Beveled antler tips (i.e., chipped or slight wear caused by polishing), cracks, and other antler imperfections were not included as antler breakage because they did not affect the overall appearance or apparent function of the antler (Jin and Shipman 2010).

We obtained precipitation data from the nearest National Oceanic and Atmospheric Administration weather station in Troy, Alabama (42 km southeast; National Climatic Data Center 2010). Though we recovered shed antlers during the subsequent calendar year in which they were grown, we matched precipitation data to the year in which antlers were grown but not shed. We used logistic regression to explore the effects of annual and growing season (April–September) precipitation on the probability of antler breakage. Also, we used logistic regression (binomial response value of 1 = broken antler and value of 0 = intact antler) and evaluated a set of models relating the effects of total antler points, typical antler points, and beam circumference to probability of antler breakage and ranked models using AIC (Akaike's information criteria; Burnham and Anderson 2002).

To determine if certain antler points were more or less likely to break, we used logistic regression (binomial response value of 1 = broken antler tine and value of 0 = intact antler tine). We included antler tine (i.e., G1…G4) as a categorical variable and individual shed antler as a random effect. By examining the interaction term between number of typical antler points and individual antler tine, we could differentiate whether or not a G3 antler point was more likely to break when it was the leading tine on an antler with four typical points versus when it was protected by a G4 antler point on a shed antler with five typical antler points. Spikes and six-point antlers were omitted from analysis due to low sample size ($n = 6$ and $n = 6$, respectively). Also, we used linear regression to examine the relationship between year (years 2000–2009) and variables beam circumference, total points, and typical points. We used Program R (R Development Core Team 2009) for statistical analyses, and α was considered significant at <0.05.

Results

We collected 487 shed antlers from 2001–2010 of which 147 (30%) exhibited antler breakage (Figure 1). The number of typical and total antler points remained similar between years. In 2000–2001, average beam circumference was 94.4 ± 1.4 mm ($\bar{x} \pm$ SE)
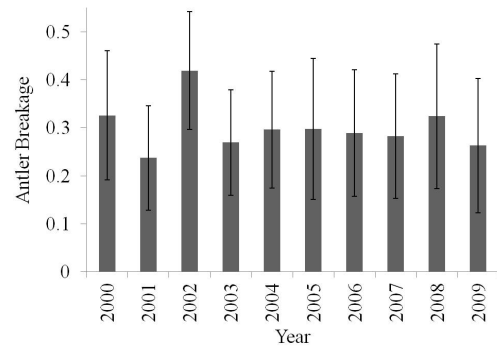

Figure 1. Annual antler breakage rates calculated from white-tailed deer shed antlers, Three Notch, Alabama, 2000–2009 (error bars represent SE).

Table 1. Factors influencing the probability of white-tailed deer antler breakage, Three Notch, Alabama, 2000–2009.

Model	n parameters	ΔAIC_c[a]	AIC_w[b]
S (beam circumference + total antler points)	3	0.00	0.374
S (beam circumference + typical antler points)	3	0.652	0.270
S (global model – all 3 parameters)	4	1.667	0.163
S (beam circumference)	2	2.507	0.107
S (constant)[c]	1	4.598	0.038
S (total antler points)	2	5.559	0.023
S (typical antler points)	2	6.390	0.015
S (total antler points + typical antler points)	3	7.314	0.010

a. Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.
b. AIC_w relative weight attributed to model
c. Model of no effects on probability of antler breakage

and increased to 102.0 ± 1.7 mm during 2002–2009 ($F_{1, 485} = 20.11$, $P < 0.001$). For the entire study period, average number of typical and total antler points were 3.93 and 4.16, respectively. Overall, beam circumference ranged from 45–174 mm, and the maximum number of typical and total points was 6 and 9, respectively.

The best model examining probability of antler breakage included beam circumference (model averaged $\beta = -0.016$) and total number of antler points (model averaged $\beta = 0.169$)—variables with negative and positive effects, respectively (Table 1). Typical number of antler points was a redundant subset of total number of antler points. Total number of antler points had a greater effect than typical antler points in the global model (all three antler variables included) and a greater relative importance weight (total number of antler points was 1.23 times as likely to be included in best model as typical number of antler points). The model containing only beam circumference and total number of antler points was best ($AIC_c = 593.9$), though two additional models had AIC_c values within 2 ΔAIC_c (Table 1). In the three top models ranked by AIC_c values, beam circumference was included in every model (relative importance weight = 0.91).
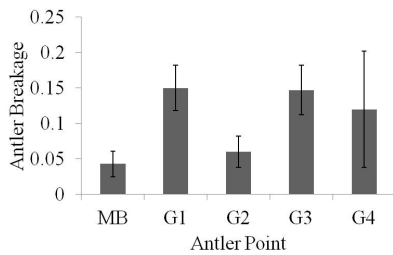
Figure 2. Antler breakage rates for main beam and individual antler points of white-tailed deer shed antlers, Three Notch, Alabama, 2000–2009 (error bars represent SE).

Neither annual precipitation ($\beta = -0.008$, $Z = -0.713$, $P = 0.476$) nor growing season precipitation ($\beta = -0.007$, $Z = -0.677$, $P = 0.498$) had an effect on annual probability of antler breakage.

Our analysis of antler breakage patterns indicated that G2 antler points were less likely to break than all other antler points. Probability of main beam breakage (0.043) was less than that experienced by all individual antler points except the G2 (0.060; $X^2_1 = 33.851$, $P < 0.001$; Figure 2). In analysis of whether or not specific antler tines were more prone to breakage dependent on number of typical points on the antler, the interaction effect was not significant. Though strictly typical antlers did not experience greater breakage than antlers possessing non-typical points ($X^2_1 = 0.068$, $P = 0.795$), typical points (0.110) were more prone to breakage than non-typical points (0.049; $X^2_1 = 6.999$, $P = 0.008$).

Discussion

Based on our overall reported antler breakage rate (30%), the estimated percentage of individual males with at least one broken antler would be 51% and is likely greater than for the majority of free-ranging populations. The white-tailed deer population we examined experienced considerable antler damage in relation to previous hypotheses made for family Cervidae (Henshaw 1971), though not as extreme as the aforementioned tule elk study (82%; Johnson et al. 2005). Our observations were comparable to antler breakage in another enclosed deer population (Ozoga and Verme 1982). The high density and male-skewed sex ratio of the study population probably increased the frequency of sparring and fighting matches between conspecifics. We hypothesize that female-biased populations with fewer older males would have lower occurrence of antler breakage. Though the proportion of males suffering breakage may fluctuate significantly between populations due to different herd demographics, nutritional deficiencies, or behavioral differences, morphological breakage patterns (e.g., which points are most/least likely to break) should remain relatively constant.

We found that beam circumference and total number of antler points were the best predictors of antler breakage. Deer possessing antlers with greater numbers of antler points and smaller-diameter antlers experienced greater rates of breakage. Because basal circumference is positively correlated with age (Roseberry and Klimstra 1975), it may be that younger deer with above average number of total antler points are most prone to breakage. Older individuals with increased spongiosa due to larger-diameter antlers were able to better absorb forces experienced during breeding season behaviors. All antler points (except G2 point) break at similar frequencies, so antlers with four or five total antler points are at greater risk of antler breakage than antlers possessing two or three points simply because there are more opportunities for breakage to occur. Number of typical antler points (relative importance weight = 0.46) is also a good predictor of antler breakage though it is redundant to total number of antler points (relative importance weight = 0.57). Seemingly similar traits, the model averaged parameter coefficient for total number of points (0.169) was greater than that of typical number of antler points (0.088). Older males are more likely to have non-typical points (Ditchkoff et al. 2000); therefore, total number of antler points may have greater explanatory power because older males may be more likely to engage in fighting. Another possible explanation is that prominent non-typical points may induce abnormal torque or strain on antlers causing increased breakage rates.

In our study, precipitation levels did not have an effect on annual antler breakage rates, though, the effect of rainfall may have been masked because deer had year-round access to supplemental protein pellets. Even during growing seasons of low rainfall, precipitation levels are normally sufficient to produce adequate quantity of deer forage to maintain healthy antler growth in the Southeast (Shea et al. 1992, Bonner and Fulbright 1999). Conversely, white-tailed deer and other cervid species living in semi-arid climates may experience suppressed antler development (e.g., smaller-diameter antlers) during extended drought periods which may lead to greater antler fragility and increased rates of breakage because of decreased forage availability (Marburger and Thomas 1965, McDonald et al. 2005).

It would seem that the G1 antler point is the most protected of all antler tines though functionally the G1 antler point is designed to stop an opponent's antlers from delivering a direct blow to the deer's skull (Goss 1990). Therefore, it is surprising that the G1 antler point was as likely to fracture as a G3 or G4 antler point receiving the majority of direct blows during intrasexual conflicts and is not more resilient to breakage given its important role. Though it probably does receive less direct contact than other antler tines, the G1 antler tine is the most mineralized of all antler tines (Miller et al. 1985), and the shortage of spongiosa may be partially responsible for our finding that it is as likely to fracture as other tines. An antler's G2 point was least susceptible to breakage. The G2 antler point is usually the longest tine on a given antler and serves as

the primary weapon when the deer's head is lowered towards a competitor (Allen 1901). Logically, the standard four- or five-point antler configuration of an adult white-tailed deer provides at least one leading antler point (G3 and/or G4 antler point) which may deflect away the impacts of fighting and protect the integrity of the G2 antler point at the expense of the G3 and/or G4 point being broken. Interestingly, our analysis revealed that G4 points did not reduce the corresponding G3 antler point's likelihood of antler breakage in five-point antler configurations.

Main beams experienced less breakage than antler points. In addition to preserving the basic functionality of the antler, the main beam and G2 antler point are the most visually prominent features of a lateral antler profile—a critical component for how males assess the quality of their competitors (Ditchkoff et al. 2001). White-tailed deer antlers develop several months before the onset of the breeding season, and asymmetry due to antler breakage could indicate a male's poor competitive ability to rival males and potential mates alike. Though the theory of fluctuating asymmetry is primarily driven by how evenly both sides of a bilateral ornament is developed by an individual, antler breakage may be another mechanism of how quality is conveyed between competitors. Intense white-tailed deer management schemes leading to unnaturally high breakage rates could potentially shift gene flow away from males possessing antlers that are susceptible to breaking if female mate selection is at least partially predicated on male quality advertisement through antlers (Ditchkoff et al. 2001).

The shed antlers collected during the first two years of study had smaller dimensions than those collected later. Because the high fence was erected in 1997, the number of mature males ($\geq$5.5 years old) possessing antlers that reached their full potential did not stabilize until at least 2001. Interestingly, antler breakage peaked at 43% in 2002. Though purely speculative, we hypothesize that fighting may have increased in frequency due to the growing population density of mature males and the relative scarcity of breeding females as compared to previous years. Ozoga and Verme (1982) documented a similar pattern where antler breakage increased from virtually zero to a rate of 34% as the density of adult males increased in a captive white-tailed deer herd. Their findings lend additional evidence that herd demographics play an important role in antler breakage.

Breakage is likely a byproduct of the antler's characteristics, the individual's behavior and social status, demographics at the subpopulation level, and possibly external environmental variables. The general patterns of antler breakage that we reported for a high density, male-dominated population further describe the intricacies of Cervidae weaponry and provide a different perspective for the oft observed (Henshaw 1971) yet seldom studied phenomenon

of antler breakage in white-tailed deer. Our results suggest that food supplementation may alleviate antler breakage in years of drought when antler circumference may otherwise decrease because of limited resources and reduced antler growth. White-tailed deer managers (especially where trophy antler quality is a primary objective) should be aware that as management intensity increases, increased probability of antler breakage may be a concurrent consequence—an important detriment to the goal of maximizing trophy antler potential. Lastly, state agencies that place antler point harvest restrictions (e.g., Pennsylvania; Norton et al. 2012) on male white-tailed deer should attempt to understand how antler breakage patterns can potentially reduce the number of eligibly harvested males in a population, thereby affecting harvest goals.

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