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Original Article

Effects of Restrictive Harvest Criteria on Antler Size of Hunter-harvested Male White-tailed Deer and Hunter Opportunity

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ABSTRACT Antler-based selective harvest criteria (SHC; e.g., number of points) are a commonly used and effective method of limiting harvest of 1.5-year-old male white-tailed deer (*Odocoileus virginianus*). However, previous research has shown SHC that allow disproportionate harvest of young males with large antlers may reduce average antler size within older (≥2.5-yr) age classes. We used hunter-harvest data collected from 10 wildlife management areas in Georgia, USA, during 2003–2013 to compare cohort antler size and other factors among areas with varying or no SHC. Three of the areas restricted harvest to males with one antler beam ≥41 cm long or an antler spread ≥38 cm (BS), and another 3 restricted harvest to males with ≥4 antler points on one side (4OS). Any male with visible antlers was eligible for harvest on the remaining areas. There was no evidence that either BS or 4OS criteria led to a decrease in antler size of harvested males ≥2.5 years old. Both SHC protected ≥96% of 1.5-year males from harvest. There was also evidence to suggest the BS criteria increased mean antler size of harvested males and annual harvest rates of 3.5-year males. However, the 4OS criteria protected 49%, 16%, and 9% of 2.5, 3.5, and ≥4.5-year males, respectively. The BS criteria protected 77%, 33%, and 10% of the same age classes. These findings suggest restrictive SHC can prevent decline in antler size of harvested males and increase opportunity for hunters to harvest older males with larger antlers, with the added biological benefit of increasing the population age structure. However, restrictive SHC may unintentionally protect a significant proportion of ≥2.5-year males from harvest. As previously suggested, managers interested in SHC should carefully research site- and age-specific antler size to avoid implementation of criteria that are either too restrictive or permissive. © 2019 The Wildlife Society.

KEY WORDS antler restriction, antler size, Georgia, harvest, hunter, *Odocoileus virginianus*, selective harvest criteria, white-tailed deer.

Antler-based selective harvest criteria (SHC) are commonly used to limit hunter harvest of subadult (1.5-yr-old), male white-tailed deer (*Odocoileus virginianus*). At least 23 states in the United States and 1 Canadian province utilized some form of SHC in 2017. Selective harvest criteria vary considerably among jurisdictions, but often limit harvest of males to those meeting some minimum measurement related to the number of antler points, antler spread, main beam length, Boone and Crockett score, or a combination thereof (Quality Deer Management Association 2018). The biological objective of SHC is to address the skewed male age structure associated with populations where hunter harvest of subadult males is high. From a social perspective, the objective of SHC is to provide hunters with increased opportunity to harvest large-antlered adult males.

Monitoring of outcomes associated with implementation of SHC has been generally lacking (Carpenter and Gill 1987). However, Wallingford et al. (2017) reported that SHC in Pennsylvania, USA, decreased subadult male harvest rates and increased harvest of large-antlered adults. Nonetheless, using antler characteristics as an index of age may have unintended consequences because of considerable overlap of antler characteristics among age classes. For example, Shea and Vanderhoof (1999) reported SHC that allowed harvest of larger antlered 1.5-year-old males resulted in a decrease in average antler size of 2.5-year males. As a result, they suggested managers

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implement SHC that protect at least the majority of subadult males.

Strickland et al. (2001) evaluated the effects of statewide SHC in Mississippi, USA, that adhered to this recommendation; SHC protected 58–79% of 1.5-year males, depending on physiographic region. Nonetheless, they reported antler size of 2.5- and 3.5-year males declined within 3 years of SHC implementation in the region where the fewest 1.5-year males were protected by SHC; antler size of older age classes in the remaining regions declined during subsequent years (Demarais et al. 2005). Thus, it would appear that even SHC that protect 79% of 1.5-year males are insufficient to prevent selective removal of larger antlered young males from the standing crop.

In response, it may seem logical to increase the restrictiveness of SHC to a point that essentially all 1.5-year males are not vulnerable to harvest. However, there may be tradeoffs associated with this approach as well. Namely, restrictive SHC may inadvertently protect smaller antlered, older males (DeYoung 1990, Strickland et al. 2001). If so, hunter satisfaction may decline because the number of males that may be legally harvested within a population would decrease. Further, because antler characteristic heritability estimates are greater for older males, invulnerability of small-antlered older males to harvest may affect gene frequencies for antler traits in subsequent generations (Williams et al. 1994, Lukefahr and Jacobson 1998). More recently, however, Webb et al. (2011) reported that selective harvesting in free-ranging populations is unlikely to change genetic characteristics of populations. Further, Michel et al. (2016) reported antler characteristics are moderately to highly heritable regardless of sire age.

Nonetheless, effects of restrictive SHC (i.e., criteria protecting ≥90% of 1.5-yr males) on cohort-specific antler size of harvested males or other factors have not been evaluated. Therefore, we used data from a number of Wildlife Management Areas (WMAs) in the Piedmont and Upper Coastal Plain physiographic regions of Georgia, USA, to address this information gap. Specifically, we evaluated whether restrictive SHC affected mean antler size of 2.5-, 3.5-, and ≥4.5-year harvested males, the proportion of males within each cohort protected from harvest, the proportional representation of each cohort in the harvest, harvest rates by cohort, and composite antler size of harvested males. Our objectives were to determine if restrictive SHC could prevent a decline in antler size of harvested males ≥2.5 years old, and document any unintentional outcomes (i.e., protection of small-antlered older males or decrease in harvest rates) associated with restrictive SHC. We hypothesized that there would be no difference in cohort antler size among areas with no SHC and restrictive SHC, the proportion of males within each cohort protected from harvest would increase as SHC restrictiveness increased, the proportion and number of older males in the harvest would increase with restrictiveness of SHC, and composite antler size of harvested males would be greatest on the most restrictive areas.

STUDY AREA

Our data set consisted of deer harvested on 10 Wildlife Management Areas (WMAs) in Georgia. B.F. Grant, Big Lazer Creek, Blanton Creek, Cedar Creek, Joe Kurz, Rum Creek, and West Point WMAs were located in the Piedmont physiographic region; whereas, Flint River, Oaky Woods, and Ocmulgee WMAs were located in the Upper Coastal Plain physiographic region (Fig. 1). B.F. Grant was a 4,600-ha WMA primarily composed of mixed hardwood (36%) and pine (*Pinus* spp.; 35%) forests, and pastures and hay fields (14%). Big Lazer Creek was a 2,900-ha WMA primarily composed of mixed hardwood (59%) and pine (36%) forest. Blanton Creek was a 1,900-ha WMA primarily composed of pine (52%) and mixed hardwood (37%) forest. Cedar Creek was a 16,000-ha WMA primarily composed of mixed hardwood (45%) and pine (43%) forest. Joe Kurz was a 1,500-ha WMA primarily composed of mixed hardwood (39%) and pine (30%) forest, as well as pastures and hay fields (18%). Rum Creek was a 2,300-ha WMA primarily composed of mixed hardwood (41%) and pine (37%) forests, as well as grassland–herbaceous areas (12%). West Point was a 3,600-ha WMA primarily composed of pine (50%) and mixed hardwood (44%) forests. Flint River was a 900-ha WMA primarily composed of pine (75%) forest. Oaky Woods was a 5,200-ha WMA primarily composed of pine (51%), mixed hardwood (25%), and mixed (22%) forest. Ocmulgee was a 6,000-ha WMA primarily composed of pine (56%) and mixed hardwood (20%) forest.

Common hardwood species on our study areas included white oak (*Quercus alba*), northern red oak (*Q. rubra*), southern red oak (*Q. falcata*), post oak (*Q. stellata*), water oak (*Q. nigra*), red maple (*Acer rubrum*), pignut hickory (*Carya glabra*), shagbark hickory (*C. ovata*), mockernut hickory (*C. tomentosa*), and sweetgum (*Liquidambar styraciflua*). The predominant pine species was loblolly pine (*Pinus taeda*). Upland pine stands were periodically harvested to thin or regenerate the stand, and treated with prescribed fire every 3–5 years. Open areas were primarily maintained via periodic mowing or grazing.

The average summer temperature in central and south Georgia was approximately 27° C, and the average winter temperature was 9° C. Temperatures during spring and autumn were more variable. Total annual precipitation was approximately 114 cm (National Climatic Data Center 2014).

METHODS

The WMAs in our study were grouped into 1 of 3 categories in terms of SHC. On B.F. Grant, Flint River, and Joe Kurz WMAs, only males with a main antler beam ≥41-cm long, or an outside antler spread ≥38 cm (beam/spread [BS]) were legally eligible for harvest. On Big Lazer Creek, Blanton Creek, and West Point WMAs, only males with ≥4 antler points on one side, each ≥2.5 cm in length, (4-on-a-side [4OS]) were legal for harvest. Any male with visible antlers above the hairline was legal for harvest on Cedar Creek, Oaky Woods, Ocmulgee, and Rum Creek WMAs. During

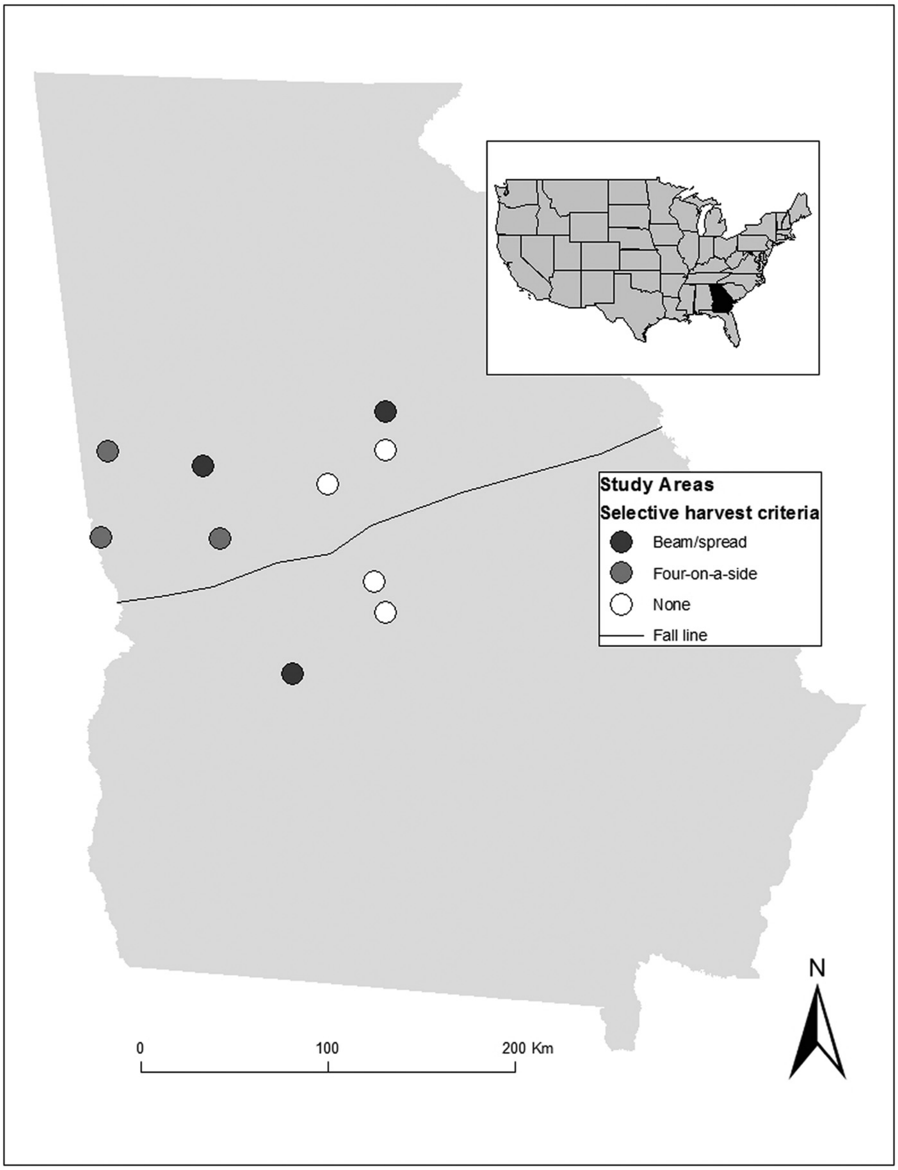

Figure 1. Locations of Wildlife Management Areas in Georgia, USA, where data were collected during 2003–2013 to determine the effects of 2 antler-based selective harvest criteria on cohort-specific antler size of white-tailed deer. Areas to the north and south of the Fall Line are in the Piedmont and Upper Coastal Plain physiographic regions, respectively.

the study period (2003–2013), hunters were required to bring all deer to the area check station immediately after harvest.

For each deer, biologists measured the basal diameter, main beam length, outside spread, and number of points for the antlers, and estimated the deer's age using tooth replacement and wear patterns (Severinghaus 1949). We created an index of antler size similar to Strickland et al. (2013) by summing the 4 antler measurements, and assigned each male in the data set to 1 of 3 selective harvest criteria (i.e., none, BS, 4OS), depending on regulations where they were harvested. We separated 2.5- and 3.5-year deer by age class and pooled deer ≥4.5 years old. To standardize the data set, we omitted males ≥2.5 years that did not meet both the BS and 4OS criteria, regardless of the SHC where they were harvested, as in Strickland et al. (2001).

We also expected variation in antler size due to sampling location (i.e., WMA) and year; therefore, we used the nlme package in the Program R software to fit linear mixed-effects models to these data (R Core Team 2015, Pinheiro et al. 2017). Specifically, we treated the interaction between SHC and age class as a fixed effect; site was nested within year as a random effect. We also pooled the antler-size index data across age classes and used a mixed-effects model with the same random effects structure to examine the main effect of SHC on overall antler size of males in the harvest. We set $\alpha = 0.05$. Although this analytical approach accounts for similarity in observations within a year and site, which also decreases the potential for site- and cohort-specific factors to confound results, SHC were not randomly assigned to each WMA and effects of SHC on antler size may have been confounded by inherent differences in productivity among sites. Therefore, similar to Strickland et al. (2001), we compared body mass of yearling, nonlactating females among each SHC as an independent indicator of environmental variation. For this analysis we used a linear mixed-effects model with yearling female body mass as the response variable, SHC and Julian date of harvest as fixed effects, and site nested within year as random effects.

We used uncensored data from the 4 areas with no SHC (i.e., any antlered male was legal to harvest) to estimate the percentage of males in each age class that would be legal for harvest in this region under the BS and 4OS criteria. To enable comparison of our results to a similar study (Strickland et al. 2001), we also estimated the percentage of males in each age class protected from harvest under a SHC where only males with ≥4 total antler points ≥2.5-cm long (4 total points [4T]) could be harvested. We used chi-square tests to determine whether the proportion of males protected by each SHC differed within an age class. This required 3 chi-square tests/age class, so we used the Bonferroni correction and set $\alpha = 0.017$.

The objective of SHC is to decrease the proportion of 1.5-year males and increase the proportion of older males in the harvest, so we also calculated the proportion of each age class in the harvest for each SHC. We calculated the proportion of each age class in the hunter harvest during each year for each WMA in the data set for this analysis. We transformed proportions on the logit scale and used linear regression with the interaction between SHC and age as fixed effects. However, by default, a decrease in 1.5-year males in the harvest will increase the proportion of ≥2.5-year males in the harvest, even if the actual number of older males in the harvest remains unchanged. Thus, we also compared annual harvest per 405 ha, by age class, among each SHC, with the interaction between SHC and age as fixed effects (Demarais et al. 2005). Finally, we used linear regression to estimate composite antler size of harvested males (regardless of age) as a function of SHC. Site was nested within year as random effects in all models to account for the data structure and unknown sources of variation among sites and years.

RESULTS

Hunters harvested 1,519 male deer that met our minimum antler criteria across the 11 study areas from 2003 to 2013. On BS areas, hunters harvested 154 2.5-year males, 203 3.5-year males, and 128 males ≥4.5 years that met our criteria. On 4OS areas, hunters harvested 61 2.5-year males, 152 3.5-year males, and 113 ≥4.5-year males that met our criteria. On areas with no antler restrictions, hunters harvested 159 2.5-year males, 320 3.5-year males, and 223 ≥4.5-year males that met our criteria. Our data set also included 790 hunter-harvested yearling female deer: 162 from 4OS areas, 182 from BS areas, and 446 from areas with no antler restrictions. Finally, our data set included 2,574 hunter-harvested yearling male deer: 33 from 4OS areas, 28 from BS areas, and 2,513 from areas with no antler restrictions.

Yearling female body mass was similar between BS and no SHC areas, but was approximately 2.7 kg lower on 4OS areas compared to no SHC areas (Table 1). Julian date was positively related to yearling female body mass. As expected, antler-size index of harvested males increased with age (Table 2). There was no evidence to support an effect of the 4OS criteria on antler-size index within an age class. However, on average, hunters harvested larger antlered males on areas with BS criteria. There was also a significant interaction between the BS criteria and ≥4.5-year age class. Based on visual interpretation of parameter estimates and associated confidence intervals, hunters harvested larger antlered 2.5- and 3.5-year males on areas with BS criteria, but there was no difference in antler size of ≥4.5-year males among the 3 SHC (Fig. 2a). However, composite antler-size index (i.e., age classes pooled) of harvested males was greatest on BS, but similar between 4OS areas and those with no SHC (Table 3; Fig. 2b).

Table 1. Parameter estimates, lower (LCL) and upper (UCL) 95% confidence limits, and *P*-values ($\alpha = 0.05$) estimated by a linear regression model for 1.5-year-old female white-tailed deer body mass (kg) harvested on areas with differing selective harvest criteria (SHC) for males based on antler characteristics. Data were collected from wildlife management areas in the Piedmont and Upper Coastal Plain physiographic regions of Georgia, USA, 2003–2013. The intercept is the estimated body mass for yearling females on areas with no SHC and parameter estimates for beam/spread and 4OS represent the change in body mass from that reference condition.

Parameter	Estimate	LCL	UCL	*P*
Intercept[a]	26	19	32	<0.001
Beam/spread[b]	−0.35	−1.7	1.0	0.61
4OS[c]	−2.7	−4.06	−1.4	<0.001
Julian date[d]	0.023	0.0030	0.043	0.02

[a] Males subject to no selective harvest criteria.

[b] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

[c] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

[d] Julian date female was harvested.

The estimated percentage of males from unrestricted areas that would have been protected from harvest by each SHC

Table 2. Parameter estimates, lower (LCL) and upper (UCL) 95% confidence limits, and *P*-values ($\alpha = 0.05$) estimated by a linear regression model for antler size index (cm) of white-tailed deer, by age class, harvested in areas with differing selective harvest criteria based on antler characteristics. Data were collected from wildlife management areas in the Piedmont physiographic region of Georgia, USA, 2003–2013.

Parameter	Estimate	LCL	UCL	*P*
Intercept[a]	101	100	103	<0.001
Beam/spread[b]	3.7	1.7	5.7	<0.001
4OS[c]	0.6	−2.0	3.2	0.64
3.5 yr old	6.9	5.3	8.6	<0.001
≥4.5 yr old	16	14	18	<0.001
Beam/spread × 3.5	−0.8	−3.2	1.7	0.54
4OS × 3.5	−1.4	−4.4	1.6a	0.37
Beam/spread × ≥4.5	−3.7	−6.4	−1.0	0.007
4OS × ≥4.5	−1.0	−4.2	2.2	0.54

[a] 2.5-yr-old males subject to no selective harvest criteria.

[b] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

[c] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

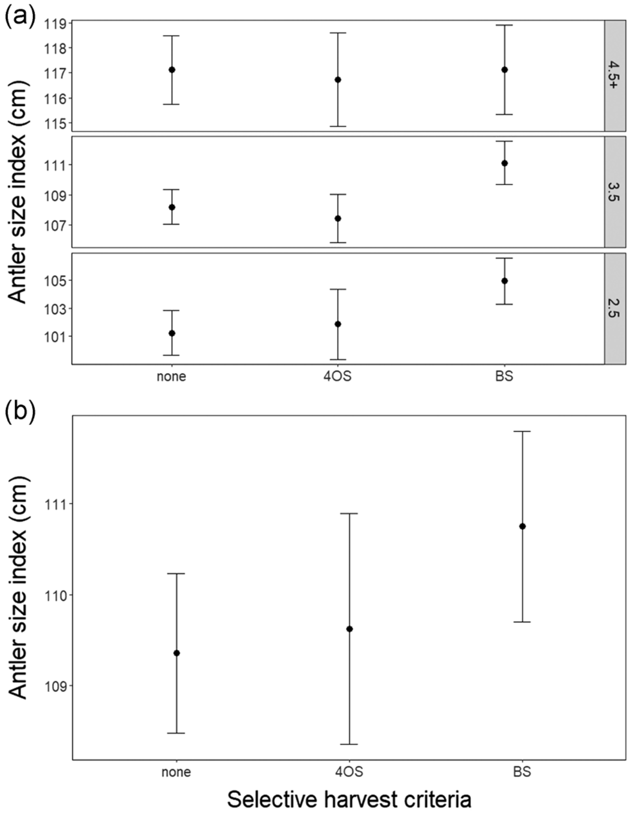

Figure 2. Cohort-specific (a) and overall (b) antler-size index of hunter-harvested male white-tailed deer as a function of antler-based selective harvest criteria. Data were collected from hunter-harvested deer on 10 Wildlife Management Areas in central Georgia, USA, during 2003–2013. Four of the areas allowed harvest of any male with visible antlers (none), 3 of the areas restricted harvest to males with ≥4 antler points on one side, each ≥2.5 cm in length (4OS), and the remaining 3 restricted harvest to males with a main antler beam ≥41-cm long, or an outside antler spread ≥38 cm (BS).

varied among age classes and SHC (Table 4). For 1.5-year males, 4T would have protected fewer males from harvest than 4OS or BS. The estimated proportion of 2.5- and 3.5-year males protected from harvest would have varied among all 3 SHC. Finally, 4T would have protected fewer ≥4.5-year males from harvest than either 4OS or BS.

The hunter harvest on areas with no SHC consisted of a greater proportion of 1.5-year males, whereas proportional harvest of 2.5-year males was similar among SHC. However, proportions of 3.5- and ≥4.5-year males in the harvest was greater on 4OS and BS areas than on areas with no SHC (Table 5; Fig. 3a). Harvest density of 1.5-year males followed a similar trend; hunters harvested 3.3 1.5-year males/405 ha on areas with no SHC versus 0.16 and 0.32/405 ha on 4OS and BS areas, respectively (Table 6; Fig. 3b). However, the lower harvest density of 1.5-year males on 4OS and BS areas did not directly translate to increased harvest densities of older males. For example, harvest density of 2.5-year males was similar among all SHC. There was also confidence interval overlap for harvest density of

Table 3. Parameter estimates, lower (LCL) and upper (UCL) 95% confidence limits, and *P*-values ($\alpha = 0.05$) estimated by a linear regression model for antler size index (cm) of white-tailed deer, pooled across age classes, harvested in areas with differing selective harvest criteria based on antler characteristics. Data were collected from wildlife management areas in the Piedmont physiographic region of Georgia, USA, 2003–2013.

Parameter	Estimate	LCL	UCL	*P*
Intercept[a]	109	108	110	<0.001
Beam/spread[b]	1.39	0.21	2.58	0.02
4OS[c]	0.27	−1.08	1.61	0.69

[a] Males subject to no selective harvest criteria.

[b] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

[c] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

Table 4. Percentage of male white-tailed deer protected from hunter harvest by antler-based harvest criteria on wildlife management areas in the Piedmont physiographic region of Georgia, USA, 2003–2013. To avoid bias, only wildlife management areas without antler restrictions were included in this analysis. Within an age class, values with different letters are statistically different from each other.

	Males protected from harvest (%)		
Age class (yr)	4T[a]	4OS[b]	Beam/spread[c]
1.5	65A	96B	99B
2.5	8A	49B	77C
3.5	3A	16B	33C
≥4.5	1A	9B	10B

[a] Only males with ≥4 total antler points, ≥2.5 cm long, may be harvested.

[b] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

[c] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

Table 5. Logit-transformed parameter estimates, lower (LCL) and upper (UCL) 95% confidence limits, and P-values ($\alpha = 0.05$) estimated by a linear regression model for proportional representation of male white-tailed deer in the hunter harvest, by age class, in areas with differing selective harvest criteria based on antler characteristics. Data were collected from wildlife management areas in the Piedmont physiographic region of Georgia, USA, 2003–2013.

Parameter	Estimate	LCL	UCL	P
Intercept[a]	0.19	0.020	0.35	0.02
4OS[b]	−2.9	−3.2	−2.6	<0.001
Beam/spread[c]	−3.01	−3.4	−2.6	<0.001
2.5 yr old	−1.2	−1.5	−1.0	<0.001
3.5 yr old	−2.2	−2.4	−1.9	<0.001
≥4.5 yr old	−3.0	−3.2	−2.8	<0.001
4OS × 2.5	3.2	2.7	3.6	<0.001
Beam/spread × 2.5	3.3	2.8	3.8	<0.001
4OS × 3.5	4.4	3.9	4.8	<0.001
Beam/spread × 3.5	4.5	4.0	5.0	<0.001
4OS × 4.5	4.4	3.9	4.9	<0.001
Beam/spread × 4.5	4.3	3.8	4.8	<0.001

[a] 1.5-yr-old males subject to no selective harvest criteria.

[b] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

[c] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

3.5- and ≥4.5-year males on 4OS and no SHC areas (Fig. 3b). However, harvest density of 3.5-year males on areas with no SHC (0.77/405 ha) was 55% lower than on BS areas (1.70/405 ha). Harvest density of 3.5-year males on 4OS areas (1.14/405 ha) also appeared to be lower than on BS areas, but there was slight confidence interval overlap. There was also slight confidence interval overlap between harvest density of ≥4.5-year males on areas with no SHC (0.41/405 ha) versus BS areas (0.93/405 ha).

DISCUSSION

Research on the biological and social outcomes of SHC is relatively scarce considering their widespread implementation across the United States and Canada. However, the primary concern mentioned in previous reports from the Southeast is that SHC allow ‘high grading’ of the standing crop of male deer by allowing harvest of only the largest-antlered 1.5-year males (e.g., Shea and Vanderhoof 1999, Strickland et al. 2001, Demarais et al. 2005). This is a valid concern. Selective harvest criteria that protected as many as 80% of yearling males from harvest in a Mississippi population led to an eventual decrease in antler size of ≥2.5-year males (Strickland et al. 2001). In response, statewide changes were made to establish SHC that protected nearly 100% of 1.5-year males (Adams and Hamilton 2011). Although results of this change have not been published, the 2 SHC we evaluated would have protected ≥96% of 1.5-year males on areas with no SHC. We found no evidence to suggest these criteria decreased average antler size of harvested males among older cohorts. This finding is theoretically contrary to the simulation results of Strickland et al. (2001), which would predict that the highly restrictive SHC we evaluated would have simply delayed high-grading to older age classes, given that the 4OS and BS criteria protected only 49% and 77% of 2.5-year males, respectively. However, their simulation assumed equal harvest vulnerability among age classes, whereas there is evidence to suggest hunter harvest vulnerability may decrease with age (Ditchkoff et al. 2001). If that is the case, protecting males until ≥2.5 years of age may be sufficient to prevent high-grading, given that hunters cannot harvest older males as intensively as younger males.

However, cohort antler size is significantly affected by soil fertility, which differs among physiographic regions in the Southeast (Strickland and Demarais 2000). Our study areas encompassed 2 physiographic regions; therefore, nonrandom assignment of SHC could have confounded our results. We addressed this potential confound both by including site as a random effect in the model and comparing body mass among 1.5-year females harvested among areas with each SHC. If differences in soil fertility masked the negative effects of either SHC on cohort antler size, the expectation would be that yearling female body mass would be greater on 4OS and BS areas than on areas with no SHC, which was not the case. In fact, female body mass was similar between BS and no SHC areas and lower on 4OS areas than on no-SHC areas. Therefore, we are confident our results relative to cohort antler size were not affected by systematic bias in productivity among sites according to SHC.

From a management perspective, however, the primary objective of SHC is typically to protect 1.5-year males from harvest. Both SHC in our study were highly effective in achieving this objective, similar to prior reports (Shea and Vanderhoof 1999, Strickland et al. 2001, Demarais et al. 2005, Wallingford et al. 2017). In addition, both the 4OS and BS criteria were effective at increasing the proportion of older males in the harvest, which is often also an objective of SHC. However, Demarais et al. (2005) cautioned that a SHC-driven shift in age composition can be explained mathematically by removal of 1.5-year males from the harvest. Instead, they suggested success of SHC should be measured according to their effectiveness at increasing actual harvest rates of older males. Their work in Mississippi suggested harvest rates of 2.5-year males did not change post-SHC and there was only a modest increase in harvest of ≥3.5-year males, very similar to our findings. In contrast, Wallingford et al. (2017) reported that SHC reduced harvest rates of 1.5-year males and increased harvest rates of ≥2.5-year males with larger antlers in Pennsylvania.

Nonetheless, we argue that using only age-specific harvest rates to measure success of SHC conflates the biological and social objectives of SHC. Specifically, it is not necessary for harvest rates of ≥2.5-year males to increase for a deer population to experience the biological benefits of a more balanced male age structure such as an earlier, temporally concentrated, breeding season (Miller et al. 1991, Jacobson 1992). It is important, however, that harvest rates increase if SHC are implemented with the social objective of providing increased opportunity to harvest older males. Our data suggest this was at least partially true for the SHC we evaluated, but it is possible that the full effects of SHC on harvest rates of mature males are not realized because of inadvertent protection of some mature males from harvest.

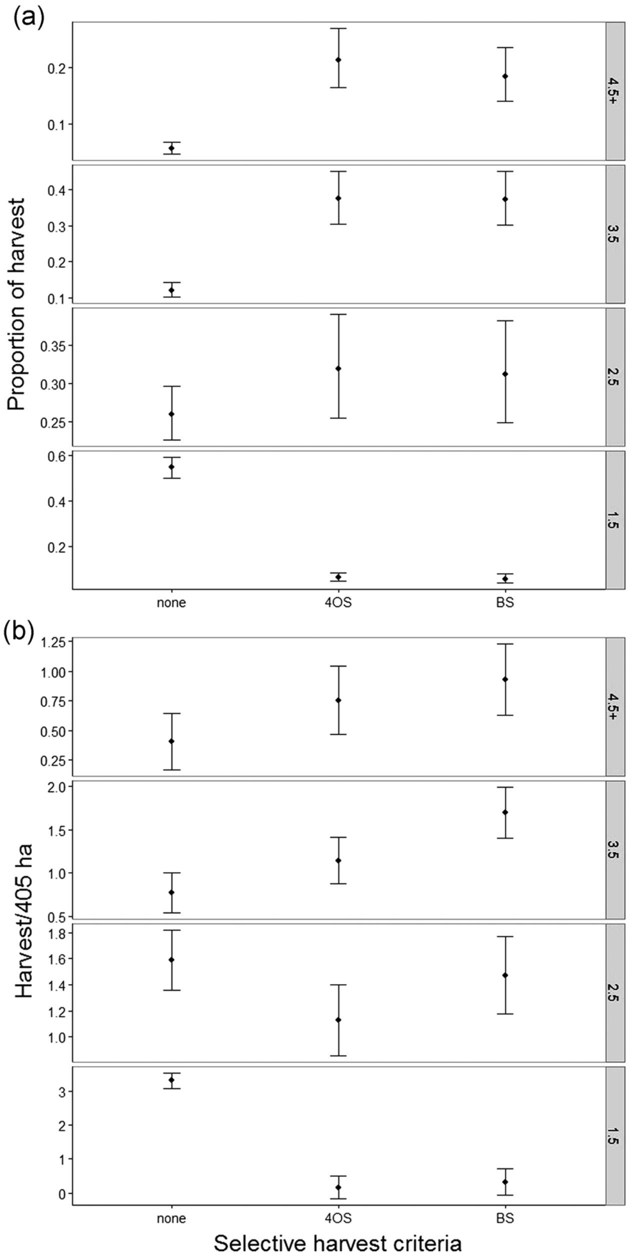

Figure 3. Proportion of harvest (a) and harvest rates (b) for male white-tailed deer on 10 Wildlife Management Areas in Georgia, USA, during 2003–2013. Four of the areas allowed harvest of any male with visible antlers (none), 3 of the areas restricted harvest to males with ≥4 antler points on one side, each ≥2.5 cm in length (4OS), and the remaining 3 restricted harvest to males with a main antler beam ≥41-cm long, or an outside antler spread ≥38 cm (BS).

Logically, as SHC become more restrictive, the number of males with antlers never meeting those criteria will increase. For example, relatively lax SHC that only protected males with <4 total antler points in Mississippi protected approximately 25% of 2.5-year males, 5% of 3.5-year males, and 4% of ≥4.5-year males in the physiographic region with the smallest average antler size (Strickland et al. 2001). The SHC we evaluated were even more restrictive, protecting a greater proportion of all males ≥2.5 years old. Thus, we suggest future work should focus on the tradeoffs between protection of yearling males and inadvertent protection of mature males when maximizing mature male harvest is the primary objective.

Antler size is positively related to male age in white-tailed deer, so restricting harvest to older males may also satisfy the social objective of increasing composite antler size of harvested males. In fact, composite antler size among harvested males was greatest on areas with the most restrictive SHC we evaluated, BS. However, confidence limits of composite antler score estimates for males harvested on 4OS versus BS areas significantly overlapped. Wallingford et al. (2017) considered SHC supported by the majority of hunters to be socially successful. They also noted that simple SHC regulations can be easily followed in hunting situations and readily understood by hunters to minimize unintentional violations. Presumably, as complexity of SHC

Table 6. Parameter estimates, lower (LCL) and upper (UCL) 95% confidence limits, and *P*-values ($\alpha = 0.05$) estimated by a linear regression model for harvest density (no. harvested/405 ha) of male white-tailed deer in areas with differing selective harvest criteria based on antler characteristics. Data were collected from wildlife management areas in the Piedmont physiographic region of Georgia, USA, 2003–2013.

Parameter	Estimate	LCL	UCL	*P*
Intercept[a]	3.3	3.1	3.5	<0.001
4OS[b]	−3.1	−3.5	−2.8	<0.001
Beam/spread[c]	−3.0	−3.4	−2.6	<0.001
2.5 yr old	−1.7	−2.0	−1.5	<0.001
3.5 yr old	−2.5	−2.8	−2.3	<0.001
≥4.5 yr old	−2.9	−3.2	−2.6	<0.001
4OS × 2.5	2.7	2.3	3.1	<0.001
Beam/spread × 2.5	2.9	2.4	3.3	<0.001
4OS × 3.5	3.5	3.1	3.9	<0.001
Beam/spread × 3.5	3.9	3.5	4.4	<0.001
4OS × 4.5	3.5	3.1	3.9	<0.001
Beam/spread × 4.5	3.5	3.0	4.0	<0.001

[a] 1.5-yr-old males subject to no selective harvest criteria.

[b] Only males with ≥4 points, ≥2.5 cm or longer, on one side of the antlers may be harvested.

[c] Only males with 41-cm main beams or a 38-cm outside spread may be harvested.

increases, hunter support for those criteria may decrease. Thus, the lack of evidence for a significant increase in composite antler score of the harvest from the 4OS to the BS criteria may not be justified by the increased difficulty of estimating beam length or antler spread. Considering that there was no evidence to suggest the proportion of 1.5-year or ≥2.5-year males in the harvest differed between these SHC, that harvest rates of ≥2.5-year males differed between these SHC, and that the BS inadvertently protected a greater proportion of ≥3.5-year males, it seems unlikely that the increase in complexity and restrictiveness associated with the BS criteria is justified.

MANAGEMENT IMPLICATIONS

Our results suggest that degradation of antler size of hunter-harvested, male, white-tailed deer ≥2.5 years old (one of the most common concerns associated with SHC in the literature) can be avoided by choosing SHC that protect approximately ≥95% of 1.5-year males in the population. Such regulations are likely to confer a biological benefit by improving representation of older males in the population and social benefits of increasing harvest rates of mature males and average antler size of hunter-harvested deer. However, such restrictive SHC also have important social implications such as making regulations more difficult for hunters to follow while conferring a relatively minor increase in composite antler score among harvested males. Thus, managers should carefully consider the relative importance of both biological and social objectives and attempt to define the tradeoffs associated with various SHC when implementing this management strategy. From there, specifics of the criteria should be explicitly tied to regional antler measurements (Strickland and Demarais 2007). Nonetheless, as others have suggested, SHC are a short-term solution for deer populations with right-skewed age structures; long-term objectives should focus on educating hunters on aging deer based on morphometrics other than antler size (e.g., Demarais et al. 1999).

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