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MAXIMUM SUSTAINED YIELD HARVEST VERSUS TROPHY MANAGEMENT

JONATHAN A. JENKS,[1] Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings, SD 57007, USA
WINSTON P. SMITH, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Juneau, AK 99801, USA
CHRISTOPHER S. DEPERNO, Minnesota Department of Natural Resources, Farmland Wildlife Population and Research Group, Madelia, MN 56062, USA

Abstract: We examined hypotheses regarding compatibility of managing white-tailed deer (*Odocoileus virginianus*) populations for trophy males (i.e., ≥8 points) and maximum sustained yield (MSY) harvests. Harvest of white-tailed deer on Oak Ridge Reservation, Tennessee, USA, began in 1985 following 45 years of protection. We examined several harvest characteristics (e.g., age and sex composition, antler and body size of males) under the assumption that the population had attained an equilibrium during this period and hunter bias toward males was constant across years. During 1985, 273 deer were killed by vehicles on the reservation; by 1994, mortality from vehicles declined to 143 deer. During the study period, annual harvest declined from 923 to 470 deer. We suspect that although the population had attained an equilibrium, it was likely below ecological carrying capacity (*K*) because of substantial vehicle mortality. Because of the absence of predators and other sources of natural mortality, we assumed that deer–vehicle collisions prior to hunting was the primary factor maintaining the population below *K*. After the initiation of hunting in 1985, several demographic parameters indicated the population was intensively harvested: 98% of the harvest was composed of males <4 years of age, deer–vehicle mortality was reduced by 50%, and modeling indicated that the population had stabilized at 61% of the prehunt population. Average age of trophy males declined following harvest. Body size of 1.5-year-old males increased following the initial hunt but became variable over the remaining period. Proportion of trophy males harvested declined from 36% to 15% throughout the study period. Following the initial harvest, the high proportion of yearling males harvested suggests that the age distribution of males became truncated. Results from our empirical example support the hypothesis that sustained production of trophy males is a consequence of MSY of either-sex harvests when males are considered trophy with ≥8 points, when annual recruitment at MSY consistently approaches unity, and when hunters show no selectivity bias. These constraints are unlikely under current management prescriptions.

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The best management system for maximum production of trophy male deer is a controversial subject punctuated with contradictory prescriptions and much debate (Strickland et al 1994). Connolly (1981) suggested that heavy harvest associated with MSY resulted in shifts from older age distributions to predominantly younger age classes. Thus, males do not live long enough to acquire the necessary resources to grow into trophy-class animals. In contrast, McCullough (1984) argued that management at MSY results in more trophy deer than male-only harvests. Moreover, McCullough (1984) hypothesized that harvesting at MSY results in lower competition for forage resources among remaining males, which allows them to grow faster and reach trophy quality in less time. McCullough (1984) developed this hypothesis in conjunction with experiments on a captive herd at the George Reserve, Michigan, USA (McCullough 1979). He estimated MSY for deer occupying the George Reserve with empirical data collected from 1952 to 1971. Furthermore, those data were used to evaluate years where production of trophy males was greatest (McCullough 1984); years post-herd reduction had the greatest proportion of trophy deer in the harvest. He (McCullough 1984:232–233) defined a trophy deer as "those [deer] with large, heavy antlers bearing at least 4 points on either antler (eight-pointers by eastern count, which includes both antlers)." McCullough (1984) offered these findings as evidence supporting management for sustained yield as a prescription for trophy deer production.

Hypotheses proposed by Connolly (1981) and McCullough (1984) represent a striking dichotomy between time and nutrition paradigms, and demonstrate the obvious challenge deer managers

[1] E-mail: Jonathan_jenks@sdstate.edu

face in developing effective population management prescriptions. Connolly (1981) believed that time was the most important variable related to production of trophy males. Paradigms of trophy and MSY management were deemed incompatible based on simulation experiments of Anderson et al. (1974), who observed that average age of deer and trophy quality in a population declined as intensity of hunting increased. This conclusion was based on the assumption that age composition of harvest reflected that of the population. McCullough (1984) contended that nutrition, which improved dramatically when deer populations were reduced to MSY, was most important.

Few studies (e.g., Roseberry and Klimstra 1974, McCullough 1979) are available on enclosed or semi-enclosed deer populations where mandatory registration of harvested animals results in a complete census of the harvest. However, controlled empirical studies such as these are necessary to evaluate untested hypotheses, the resolution of which establishes a scientific foundation for developing effective management philosophies. We examined the hypotheses of Connolly (1981) and McCullough (1984) using harvest data from an enclosed white-tailed deer population on the Oak Ridge Reservation (ORR), Tennessee, USA. According to McCullough's (1984) hypothesis, harvest for MSY should decrease age of trophy males, increase mass of 1.5-year-old males and females, and increase proportion of trophy males (i.e., ≥8 points) harvested. Conversely, Connolly's (1981) hypothesis predicts that age structure of the population should become younger and proportion of trophy males harvested should decrease.

STUDY AREA

Oak Ridge Reservation consists of 14,980 ha within the Ridge and Valley Province of the Southern Appalachians (Mitchell 1989). Elevation ranges from about 230 to 385 m above mean sea level (Mitchell 1989). Annual rainfall averages 14 cm (Parr and Pounds 1987). The ORR is 80% forest; dominant deciduous forest is oak (*Quercus* spp.)–hickory (*Carya* spp.). Coniferous forests are composed of eastern redcedar (*Juniperus virginianus*), hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and shortleaf pine (*Pinus echinata*). Between 1947 and 1956, much of the open-field habitat was planted with shortleaf and loblolly pine (*Pinus taeda*). Other tree species include Virginia pine (*Pinus virginiana*), white ash (*Fraxinus americana*), black locust (*Robinia pseudoacacia*), red maple (*Acer rubrum*), black walnut (*Juglans nigra*), river birch (*Betula nigra*), and American sycamore (*Platanus occidentalis*; Parr and Pounds 1987). Additional woody shrubs and forbs that characterize ORR were described by Burgess (1975).

Because ORR was surrounded by a fence 3 m high, we considered the deer population to be closed to immigration and emigration. No harvest occurred on ORR between 1940 and 1985. Thus, the population was believed to have approached a stable equilibrium with its environment near *K*.

METHODS

Harvest data were collected by ORR personnel during 10 consecutive, either-sex firearms hunting seasons from 1985 to 1994. We characterized seasons by 1 2-day hunt during each of 3 months, October–December. Nine hundred permits were issued each year, and a mandatory check station was operated on the reservation during these hunts; data were collected on all harvested deer. Demographic data collected at the check station included age (Severinghaus 1949), sex, body mass, and number of antler points.

We modeled the population using demographic data and an initial population estimate of 2,700 deer, which was recommended by Tennessee Wildlife Resource Agency personnel familiar with ORR. During the study, we used harvest and vehicle kill data to estimate preharvest population size from which we determined whether subsequent harvest reduced the population to a level close to 56% of *K* (i.e., MSY; McCullough 1987). Using harvest data, vehicle kill data, and estimated populations of 2,400, 2,700, and 3,000 deer in 1985 (sex ratio 50:50), we modeled the population using variable (0.71–0.88) recruitment rates (Table 1). Estimates of 2,400 and 3,000 deer represented a ±10% buffer, which was used to ensure that the 2,700 value was a reasonable population estimate. We correlated the modeled population with vehicle kills and assumed that the greatest correlation coefficient would represent the best estimate of true population size. Sex ratios of recruitment were set at unity; sex ratios of vehicle-killed deer, which were unavailable, were calculated according to sex composition of the reconstructed population during the same year (Dumont et al. 2000). To evaluate effect of harvest at MSY on production of trophy males, we used McCullough's (1984) definition of a trophy male as having 8 points (eastern count) or better. We used harvest data over the 10-year period to calculate mean age of trophy males, average mass

Table 1. Modeled white-tailed deer population from harvest, vehicle mortality and an estimated initial population of 2,700, Oak Ridge Reservation, Tennessee, USA, 1985–1994 (modeling assumed equal sex ratios in recruitment, applied modeled population sex ratios to vehicle mortality, and applied a 0.85 recruitment rate).

	Initial population			Harvest			After harvest			Number of	*N* after	
Year	*N*	M	F	Total	M	F	*N*	M	F	vehicle kills	vehicle kills	Recruitment
1985	2,700	1,350	1,350	923	505	418	1,777	845	932	273	1,504	676
1986	2,180	1,047	1,134	660	372	288	1,520	675	846	220	1,300	622
1987	1,922	880	1,042	530	309	221	1,392	571	821	226	1,166	594
1988	1,759	764	995	507	291	216	1,252	473	779	160	1,092	585
1989	1,678	696	981	439	261	178	1,239	435	803	155	1,084	606
1990	1,690	674	1,016	440	239	201	1,250	435	815	147	1,103	617
1991	1,720	685	1,035	475	265	210	1,245	420	825	161	1,084	619
1992	1,703	665	1,038	522	287	235	1,181	378	803	158	1,023	600
1993	1,623	617	1,007	398	209	189	1,225	408	818	165	1,060	608
1994	1,668	649	1,019	494	308	186	1,174	341	833	143	1,031	634
1995	1,665	602	1,063									

of 1.5-year-old males and females, percent trophy males in the harvest, and percent 1.5-year-old males in the harvest.

Mast production data were obtained from ORR for 1988–1994. These data were collected along established mast transect routes within the reservation. Mast indices were in the form of a calculated index incorporating data on twigs, twigs with acorns, number of acorns, and percent crown producing acorns; the index ranged from 0 to 10 with acorn crop quality ranging from poor (0–2.5) to excellent (8.6–10; Whitehead 1980). These data were regressed against average mass of adult male and female harvested deer. We used a significance level of 0.10 to reduce the probability of a

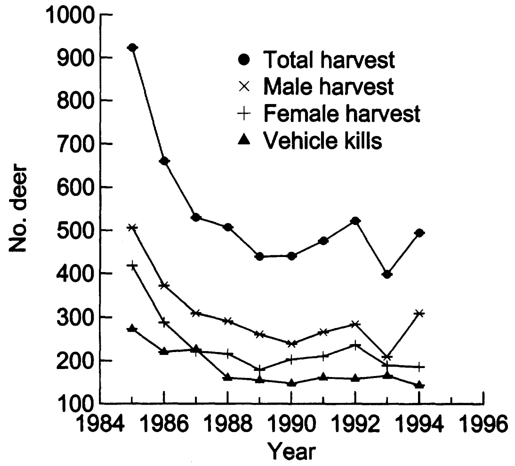

Fig. 1. Harvest (total, male, and female) and number of vehicle-killed white-tailed deer on the Oak Ridge Reservation, Tennessee, 1985–1994.

Type II error. For example, for $n = 10$ years (duration of this study) and $r = 0.67$, power increased from about 0.56 ($\alpha = 0.05$) to 0.70 ($\alpha = 0.10$).

RESULTS

From 1985 to 1994, 5,394 deer were harvested; total annual harvest ranged from 923 individuals in 1985 to a low of 398 deer in 1993 (Fig. 1). Harvest was generally stable from 1987 to 1994. During each year of the study, more male than female deer were harvested. For simulations, an initial population of 2,700 and a recruitment rate of 0.85 gave the greatest correlation coefficient (i.e., 0.93; Table 2), suggesting that harvest had stabilized the population at a posthunt population of about 1,665 individuals, which represented 61% of the prehunt population (Fig. 2). Because this estimate approached 56% (McCullough 1987), we assumed the population had stabilized near MSY. In addition, proportion of males <4 years of age increased to 98% of the harvest during the study.

Average age of trophy males declined with lowest average ages occurring from 1992 to 1994 (Fig. 3). Mean number of antler points differed ($F_{9,\ 1287} = 6.629$, $P < 0.001$) through the time series for 1.5-year-old males; the mean increased from 3.8 (± 0.16) in 1985 to 4.8 (± 0.16) in 1987. Body mass of 1.5-year-old males differed ($F_{9,\ 1287} = 8.28$, $P < 0.001$) over the time series; mass for years 1987, 1988, and 1989 were greater than in 1985 (Fig. 4). Body mass of 1.5-year-old females also differed ($F_{9,\ 544} = 2.99$, $P = 0.002$) among years, however, only mass in 1985 and 1990 differed from one another. Average male and

Table 2. Regression coefficients for relationships between modeled population size of white-tailed deer and number of vehicle-killed deer on the Oak Ridge Wildlife Management Area, Tennessee, USA, 1985–1994.

Starting N	% K[a]	Recruitment rate	Coefficient of determination	P
2,400	0	0.85	0.470	0.029
	0	0.86	0.514	0.020
	0	0.87	0.111	0.346
2,700	0	0.71	0.749	0.001
	0	0.80	0.650	0.005
	17	0.83	0.778	0.001
	62	0.85	0.872	>0.001
	85	0.86	0.651	0.005
	123	0.88	0.089	0.401
3,000	0	0.66	0.669	0.003
	27	0.68	0.790	0.001
	76	0.71	0.796	0.001
	132	0.74	0.007	0.819
	416	0.85	0.230	0.160

[a] Percent of starting population at end of time series (1995).

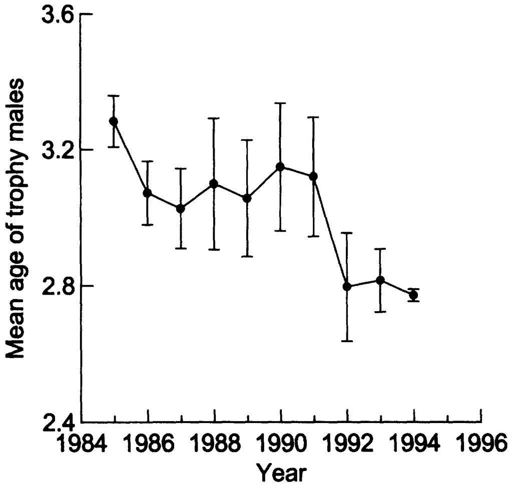

Fig. 3. Mean age of trophy male (antlers 8 point or better; McCullough 1984) white-tailed deer harvested on the Oak Ridge Reservation, Tennessee, USA, 1985–1994.

female body mass were not correlated (r^2 = 0.45, P = 0.20). Percent trophy males in the harvest declined (P = 0.009) from 36% in the first year of harvest to 21% in 1994 (Fig. 5). Percent 1.5-year-old males in the harvest increased (P = 0.080) over the time series. No relationships were found between mast production and body mass of 1.5-year-old (r^2 = 0.30, P = 0.16) or 2.5-year-old (r^2 = 0.001, P = 0.85) males. Likewise, relationships between mast lagged 1 year, and weights of 1.5- and 2.5-year-old males were not significant (1.5 year olds: r^2 = 0.02, P = 0.79; 2.5 year olds: r^2 = 0.18, P = 0.25). We correlated number of antler points with body mass of male deer >0.5 years of age by year. All relationships were highly significant (P < 0.001). Coefficients of determination ranged from 0.588 to 0.750 over the 10-year period but were not related to years post-initial harvest. Calculated sex ratio (males:100 females) declined over the 10 years of harvest (Fig. 6).

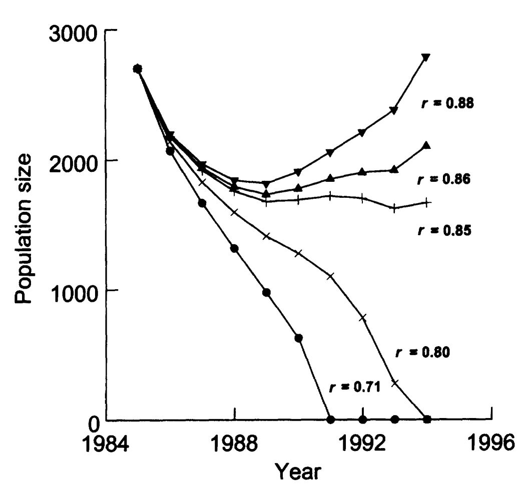

Fig. 2. Population model results for white-tailed deer on the Oak Ridge Reservation, Tennessee, USA, 1985–1994, using an initial population size of 2,700.

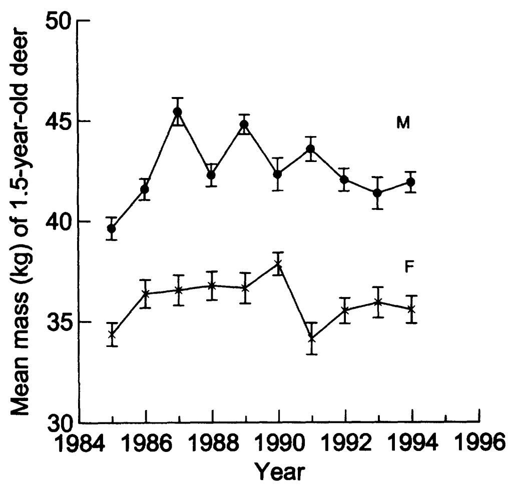

Fig. 4. Mean mass (kg) of 1.5-year-old male and female white-tailed deer harvested on the Oak Ridge Reservation, Tennessee, USA, 1985–1994.

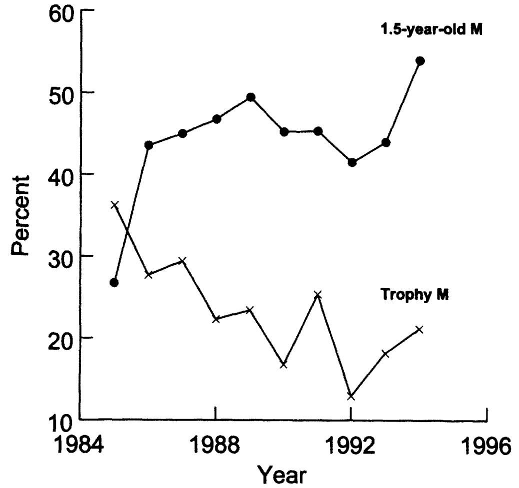

Fig. 5. Percent of trophy male (antlers 8 points or more; McCullough 1984) and 1.5-year-old male white-tailed deer harvested on the Oak Ridge Reservation, Tennessee, USA, 1985–1994.

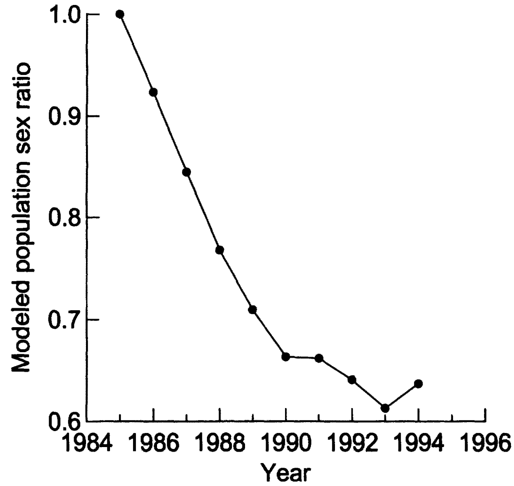

Fig. 6. Estimated sex ratio (males/100 females) for white-tailed deer on the Oak Ridge Reservation, Tennessee, USA, 1985–1994.

DISCUSSION

We tested hypotheses of McCullough (1984) and Connolly (1981) regarding compatibility of management for trophy males with management of white-tailed deer populations at MSY. However, some assumptions and limitations of our analyses may have influenced our conclusions and thus warrant further consideration. Our initial population estimate (2,700 deer) represented an average density of 18 deer/km^2, which was greater than the minimum estimate of deer density (≥12 deer/km^2) reported for this region in the mid-1980s (Barber 1984:348). Since then, however, white-tailed deer populations have increased substantially across much of their range in the East (Roseberry and Woolf 1988, McShea et al. 1997). In addition, several conditions render the ORR population unique for the region, including protection from hunting for >40 years and being enclosed, which reduces dispersal and inflates local densities.

Also, we assumed that the sex ratio of the initial, unharvested population was equal. Admittedly, unharvested populations of white-tailed deer typically show skewed sex ratios in favor of females (Smith 1981, Gavin et al. 1984). Unfortunately, no demographic data are available for the ORR deer population. But no evidence suggests that the Oak Ridge population would behave differently from other unharvested populations of white-tailed deer. In the absence of complete information, we chose an equal sex ratio. Departures from an equal sex ratio increased the female component of the population and reduced the availability of males in the population, especially when there was a male-biased harvest.

In addition, we assumed, as did Anderson et al. (1974), that changes in age and sex composition of the harvest reflected changes in the population. For this assumption to be valid, hunter bias or selectivity must be nonexistent or consistent across the period of this study. Roseberry and Woolf (1988) noted that hunter selectivity for adult males declined by 40% (i.e., from 20.8% to 12.4% of the harvest) during a 6-day hunting season. In our study, we also observed a decline (12.6%) in selectivity during the hunting season. However, selectivity was consistent among years as suggested by a correlation analysis between total harvest of females and males over the 10-year period ($r = 0.94$, $P < 0.001$).

Finally, we assumed an estimated recruitment rate of 0.85 across the time series. Admittedly, small variation in recruitment rates can result in large differences in population size. For example, in our modeling simulations (Fig. 2), a difference of 0.01 (i.e., 0.85 vs. 0.86) in recruitment rate changed the trajectory of the population from a relatively stable state to a population showing steady growth. We offer 2 lines of evidence to support our use of a constant recruitment rate of 0.85 across the period: correlation analysis of the reconstructed population with vehicle mortality data (Table 2); and a recruitment rate within the range of values reported for white-tailed deer populations approaching MSY (McCullough 1987).

Results of our population modeling indicated that harvest reduced the population to a level that approached MSY. McCullough (1987) estimated that MSY for white-tailed deer occurred at about 56% of the prehunt population. In our study, modeling indicated that the population had been reduced to 61% of the prehunt population. Although reduction in prehunt population size was variable, an increase in available forage per animal would have occurred. Thus, conditions presumably would have been favorable to observe a positive nutritional effect on development of trophy males.

The reduction in mean age of a trophy male and increase in mean number of antler points of 1.5-year-old males supported an effect of harvest on trophy production. This result also suggested that the time factor associated with trophy production was variable and possibly related to forage quality or availability. However, this variation was limited to 1 year (i.e., 2.5 to 3.5 years of age) because in this region it was unlikely that trophy class animals could be produced at 1.5 years of age. Hence, McCullough's (1984) hypothesis that a nutrition effect occurs once a population has been lowered from *K*-equilibrium is supported by this study. However, the response was limited to the youngest age (i.e., 2.5-year-old males) with a realistic expectation of becoming trophy class.

Body mass and mean number of antler points of 1.5-year-old males did increase by year 3 in the time series but became variable, with only 1 minor difference occurring in 1.5-year-old female weights. McCullough (1984) stated that when deer on the George Reserve were reduced from 126 in 1941–1942 to 10 between 1971–1975, body mass of yearling and older males increased from 66.4 to 75.9 kg, respectively. In our study, variation in body mass might be explained by variable mast production, and this relationship was positive but statistically insignificant. Furthermore, variable mast or an effect of reduced carrying capacity should affect the male and female segments of the population. Yet, body mass of harvested yearling female deer showed no trend ($P = 0.66$)and was uncorrelated ($r = 0.31$, $P = 0.373$) with male body weights. These results may not be surprising considering timing of antler development and availability of mast. Still, one might expect a benefit of mast toward increased survival of males into the population of the subsequent year. Yet, when we correlated proportion of trophy males in the population of the following year with mast of the current year, we found no evidence of increased survival for 1.5-year-old ($P = 0.79$) or 2.5-year-old ($P = 0.25$) males. Consequently, the prediction (McCullough 1984) that reduced population size would result in a consistent increase in forage availability that maintains trophy production post-initial harvest was not supported in this study. Brownlee (1975) reported similar results for desert mule deer, where mean body mass of harvested males declined (from 50 to 39 kg) as hunting pressure increased.

Production of trophy males ranged from 13 to 36% of the harvest (Fig. 5). This range is similar to that reported by McCullough (1984) for the George Reserve (14–41%). In our study, the greatest percent harvest of trophy males occurred during the first year, and it is doubtful that this percentage represents MSY of trophy males. Nevertheless, McCullough (1984) documented that 41% of the harvest of male deer on the George Reserve was classified as trophy during 1980–1981. Correlations between antler points and body weight of males (r^2 ranged from 0.588 to 0.750) also supported results from the George Reserve ($r^2 = 0.45$; McCullough 1984). Nonetheless, reduction in percent trophy males supported the prediction by Connolly (1981) that number of trophy males declines as male harvest increases.

Percent 1.5-year-old males in the harvest increased over the study, which supported the prediction by Connolly (1981) that age structure of the population becomes truncated under MSY. Although other factors, such as skewed sex ratio, reduced recruitment, and effect of variable carrying capacity on growth rates, could be implicated as causative factors associated with decreased production of trophy males, we observed no significant relationships among these variables. Therefore, we conclude that the positive nutritional effect of population reduction was not substantial enough to grow trophy deer at a sustained rate under an MSY harvest regime even with additional resources available from mast. This probably occurred because trophy deer in this region need at least 2.5 years to develop.

Our study results indicate that managing white-tailed deer populations for MSY may be compatible with sustaining trophy male harvest only under limited circumstances. During our study, average hunter selectivity for males ranged from 12.8 to 63.2% (mean = 31%), which resulted in males and females achieving 44.6 and 78.7% of the preharvest populations, respectively. One might question whether this study was a valid test of McCullough's (1984) hypothesis because females were not reduced to MSY. That is, if hunter selectivity for males was reduced to zero, females would be reduced to a level closer to MSY with a concomitant reduction in male harvest. Intuitively, this scenario seems to increase recruitment and reduce loss of potential trophy males from the population. However, when we simulated an equal harvest of males and females, the recruitment rate necessary for MSY was 0.978. Nonetheless, total annual recruitment of this simulation did not differ ($t = -0.607$, df = 9, $P = 0.522$) from the results of our population modeling. Consequently, the predicted increased nutritional benefit toward production of trophy males realized from harvesting females to MSY did not mitigate the increased total productivity of the population due to a larger number of females in the modeled population. The variance surrounding the net recruitment curve presented by McCullough (1987:544) explains this result. The expected savings (6% in this example) of males that recruit into the population of the subsequent year would likely contribute to trophy male availability. Realistically, it is unlikely that selectivity for males would be zero (Roseberry and Klimstra 1974, McCullough 1984) and could be sustained near maximum recruitment at MSY (McCullough 1987).

MANAGEMENT IMPLICATIONS

In an era when hunters are seeking more opportunities to harvest white-tailed deer without compromising the quality of males, there clearly exists a need to examine alternative management paradigms. Although intuition suggests that there must be a trade-off between maximizing total number of deer available for harvests (i.e., MSY) and managing for trophy males, compelling evidence from the literature (McCullough 1984) suggests that these 2 management objectives might not be mutually exclusive in all cases. Our empirical test of McCullough (1984) and Connolly's (1981) hypotheses revealed that although the 2 goals may not be mutually exclusive, circumstances under which MSY and trophy male production occur are limited by practical and biological constraints.

According to the empirical analysis outlined in this study, if managers seek to maximize both total deer and trophy male production under a single management prescription, deer population recruitment rates must consistently approach 1.0, and little or no selectivity must exist for males by hunters. Realistically, these conditions rarely are met, and MSY management likely will result in a decreased number of trophy males. The reasons for this pattern are clear; as Connolly (1981) predicted, the age distribution of males becomes truncated at MSY, and the proportion of older (i.e., ≥2.5-year-old) males in the population becomes negligible. Moreover, as expectations of a trophy male increase (e.g., ≥10 points, ≥ some minimum spread, and ≥ some minimum beam diameter), sustained production of trophy males under MSY becomes less likely.

In this study, we used McCullough's (1984) definition of trophy male to explicitly test his hypothesis, but hunters and wildlife professionals disagree over what constitutes a trophy. For this reason, a management program that seeks to maximize trophy males may be inherently ambiguous and difficult to evaluate. Moreover, a management objective to produce trophy males might exceed expectations of most hunters who desire an opportunity to take larger males, while disappointing many hunters who just want an opportunity to harvest any deer. Perhaps a more practical and useful management goal—one which managers will find more agreeable with a reasonable expectation of success—is the concept of managing for quality deer (i.e., ≥8 points, not Quality Deer Management [QDM], sensu Brothers and Ray 1975). Although hunters may disagree over what represents a trophy male, few would disagree that males with ≥8 points are quality deer. Clearly, the potential exists with intensive either-sex harvests that reduce populations toward MSY to increase body mass and antler points through nutritional benefits and to increase total annual harvest through sustained higher annual recruitment rates.

Therefore, managers may want to consider a management scheme that would emphasize 1 goal but not totally exclude another. For example, an either-sex hunt that requires hunters to harvest females before taking males would ensure reducing the deer population in a manner that benefits residual males nutritionally without necessarily reducing availability of quality males. Also, such a scheme might encourage hunters to be more selective in their harvest among males, thereby increasing recruitment of potential trophy males into the subsequent year's population. Creative management schemes help managers satisfy the increasing demand for trophy management and increased hunting opportunities (Ditchkoff et al. 1997). Unfortunately, expecting to sustain trophy male production while managing white-tailed deer populations for MSY will almost certainly leave both managers and hunters disappointed.

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