Relative Density–Physical Condition Models: A Potential Application for Managing White-Tailed Deer Populations

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Abstract

White-tailed deer (Odocoileus virginianus) population management is important because of this species' popularity for sport hunting and the ecological and economic damage deer can cause. Relationships between various physical condition metrics, most commonly body mass and antler measures, and estimates of absolute density have been used to develop harvest-management decision models. However, biases in estimating densities among different populations and differences in herd productivity may limit their wide-scale application. We developed models relating 3 commonly used physical parameters (yearling male body mass, yearling female body mass, and antler measures) to relative density (density/K-carrying capacity). We used these models to examine condition and density relationships among 8 populations: 1 in the midwestern and 7 in the southeastern United States. The populations studied spanned several physiographic provinces, had long-term (15- to 31-yr duration, median = 26 yr) harvest data, and varying densities (3–32 deer/km^2). Population model slopes were similar with no apparent pattern along a presumed habitat-quality gradient, suggesting that food resources, the range of relative densities, and local genetic variation may be overriding influences. However, slight variation in slopes for yearling male body mass (all between 2% and 4% change in relative density for each 0.4-kg change in mass) among populations suggests that relative density models could have general applicability in the southeastern United States. (WILDLIFE SOCIETY BULLETIN 34(4):1113–1120; 2006)

Key words

antler measures, body mass, density, density-dependence, Odocoileus virginianus*, physical condition, population management, relative density, white-tailed deer.*

The white-tailed deer (*Odocoileus virginianus*) is the most popular game animal in North America (United States Department of the Interior and United States Department of Commerce [USDI and USDC] 1993). This species generates an estimated economic value of $14 billion annually (Conover 1997). In 2001, 10.3 million hunters spent 133.5 million days hunting deer in the United States (USDI and USDC 2002). In contrast, deer (Cervidae) also cause substantial economic damage. Conover (1997) estimated crop damage conservatively to be approximately $100 million and damage by deer–vehicle collisions in excess of $1 billion per year for the United States. Other types of damage include forestry, ornamental plants, and threats to human health. In recent years attention has been focused on urban deer populations (Hansen and Beringer 1997, Nielson et al. 1997) and ecological impacts associated with excessive herbivory (DeCalesta 1997, Healy 1997, Stromayer and Warren 1997). Therefore, it is critical to provide reliable and effective tools that can be used to predict population densities and the effect of harvest-management strategies on long-term herd productivity.

Relationships between density and various physical parameters such as body mass and antler measures have been described for white-tailed deer (Johnson 1937, Jacobson 1992, Leberg and Smith 1993, Keyser et al. 2005*a*). Establishing such relationships can be a valuable

tool for making herd-management decisions by enabling managers to track density through relatively easily measured physical condition variables such as body mass or antler points (Keyser et al. 2005*a*). These same relationships also can be a valuable means for exploring density dependence in deer (Clutton-Brock et al. 1982, Leberg and Smith 1993).

One difficulty in using physical condition–density models, however, is that density measurement often can be biased for any given population (Roseberry and Woolf 1991). This problem can be magnified if different abundance estimation techniques are used (Keyser et al. 2005*a*). Thus, a model derived for one population may not be directly applicable to others.

Another weakness of models based on estimates of absolute density (i.e., deer/km^2) is they do not have any reference to carrying capacity. We define carrying capacity, or K, as the point where net recruitment reaches zero (McCullough 1979). However, no one has yet described density–physical condition relationships in such a context.

We argue that relative density, or the proportion of K-carrying capacity (McCullough 1979) represented by some absolute density, can be a useful concept for herd managers (Downing and Guynn 1985). Relative density describes position of the herd along a stock-recruitment curve, which allows a number of inferences to be drawn regarding population behavior with respect to management actions (McCullough 1984). It also allows for direct comparisons between populations with differing levels of habitat quality

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and precision in estimating absolute density. Relative density may prove to be a useful standard with a meaningful biological basis under which comparisons among populations can be reliably made. Clearly, this can be a powerful tool for herd managers.

We contend that relative density also can be used for comparing productivity levels between habitat types and range conditions and provide insights into habitat ecology issues. For instance, by monitoring changes in relative density of a herd, managers could assess the influence of substantial changes in habitat quality (e.g., clear-cutting, planting of agronomic crops, application of prescribed fire) on herd growth or productivity. Similarly, managers could compare relative densities of herds in close proximity to one another with similar soils, weather patterns, and genetics, but with different combinations of habitat types (e.g., mature hardwood vs. pine [*Pinus* spp.] plantations) and assess contributions of those habitat types to herd productivity.

Transforming the relationship between absolute density and physical parameters to one that uses relative density first requires development of an acceptable estimate of K. Where such an estimate exists, transformation of absolute density to relative density would in turn relate physical parameters directly to position along an appropriate stock-recruitment curve. Keyser et al. (2005*b*) derived stock-recruitment curves for white-tailed deer populations in the southeastern and midwestern United States based on a set of recruitment models following White and Bartmann (1997). We believe such models make it possible to develop relative density–physical condition models for those populations.

Our objective was to define relationships between various physical parameters and relative deer densities. We evaluated these relationships using data collected from white-tailed deer populations in several physiographic provinces: 1 in the midwestern and 7 in the southeastern United States.

Study Area and Methods
Criteria for selection of data sets included a minimum of 7 continuous years of data, average annual harvest of at least 100 animals, harvest data collected from a contiguous land area, age structure available through the 2.5-year age class, and traditional deer-harvest strategies that did not explicitly select against males with smaller antlers (i.e., quality deer management). The minimum number of years was important because we needed enough continuous years of data to establish multiple-year trends in density that could be associated with physical condition. Large annual sample sizes, age-structure data, and a lack of male harvest bias were needed to reliably estimate population size. Based on these criteria, we examined 7 study populations from several physiographic regions in the Southeast, including the Lower Coastal Plain (Fort Stewart, Ga. [FS]); Upper Coastal Plain (Noxubee National Wildlife Refuge, Miss. [NX], Savannah River Site, S.C. [SR]); Piedmont (Lake Russell Wildlife Management Area, Ga. [LR], Piedmont National Wildlife Refuge, Ga. [PM]); Ridge and Valley (Highland and Bath counties, Va. [HB]); and Interior Low Plateau (Land Between the Lakes National Recreation Area, Ky. [LBL]). Additionally, we also used 1 population from a region in the Midwest, the Loess Drift Hills (Crab Orchard, National

Wildlife Refuge, Ill. [CO]). The CO data set, though not typical of the Southeast, was of interest because of the exceptional habitat quality in the area (Roseberry and Klimstra 1975, Harder 1980). All 8 populations met or exceeded these criteria, particularly with respect to annual harvest size and duration of data. Collectively these populations formed the basis of broad spatial replication in what can be best described as a meta-analysis (Johnson 2002).

We made an effort to identify populations from multiple physiographic provinces because many deer managers consider them to be reasonable surrogates for habitat quality at a broad scale (Strickland and Demarais 2000, K. Kammermeyer, Georgia Department of Natural resources, personal communication, K. McCaffery, Wisconsin Department of Natural Resources, personal communication). Therefore, we sought the best available data set for the province in question and for as many provinces that had suitable data sets. The actual ordination of habitat quality among these provinces has not been empirically documented across the range of sites that we studied but seems to follow a soil fertility continuum (Jacobson 1984, Shea et al. 1992, Strickland and Demarais 2000). We examined a large number of other candidate study populations but were not able to use them for various reasons, such as presence of intensive artificial feeding, sympatric feral hog (*Sus scrofa*) populations, limited duration of harvest data, numerous gaps in harvest data, and quality-deer-management harvest guidelines. We contend that we have the best long-term data sets available across the region studied.

Using data from hunter-harvested deer, we developed population estimates based on standard reconstruction techniques as described by Downing (1980). We estimated preseason antlered male populations using 2 age classes (ages 1.5 yr and 2.5 yr and older). We estimated female and fawn numbers by a Wisconsin reconstruction (Creed et al. 1984, Roseberry and Woolf 1991). Large sample sizes were available for population reconstruction (Table 1). We converted population size to density (deer/km^2) based on the size of each respective property. We did not use the final 2 years of reconstructed population densities for each area in the analysis because they were incomplete (Downing 1980).

Because lags were demonstrated to be an important context for understanding density–physical condition relationships (Keyser et al. 2005*a*) and recruitment patterns (Keyser et al. 2005*b*), we used them as the basis for all models in this study as well. Specifically, we related physical condition for the current year to total adult (1.5 yr and older) relative density lagged 2 years. We hypothesized that density effects are manifested in this pattern (Jacobson 1992) and the fact that yearling animals were conceived 2 years earlier. Prevailing density at that time would exert a substantial influence on future condition (Verme 1965). This lag effect has been documented with respect to density-independent influences such as mast crops (Wentworth et al. 1992) and rainfall (Teer et al. 1965).

The combination of the documented influence of these factors and their lagged impact led us to implement a 3-year running average (current yr, 1 yr prior, and 2 yr prior) on both dependent and independent variables. Feldhamer et al. (1989) used such an approach to examine density-inde-

Table 1. Annual sample size and variability of data used in analysis, expressed as coefficients of variation, for 8 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998.

Population	No. of yearling M range (mean)	No. of yearling F range (mean)	Estimated relative density range (%)	Coefficients of variation (CV)		
				Yearling M weight range (median)	Yearling M antler points range (median)	Yearling F weight range (median)
Crab Orchard NWR[a], Ill.	45–213 (140)	42–136 (69)	31–78	na[b]	na	na
Fort Stewart, Ga.	18–97 (53)	5–40 (17)	50–100	na[b]	na	na
Highland–Bath counties, Va.	49–350 (163)	11–161 (64)	10–54	0.14–0.18 (0.16)	0.43–0.50 (0.47)	0.13–0.22 (0.15)
Lake Russell WMA[c], Ga.	48–143 (93)	5–46 (23)	16–52	0.15–0.16 (na[d])	0.34–0.35 (na)	0.15–0.15 (na)
LBL[e]—Ky. section only	120–410 (260)	8–232 (76)	38–78	0.12–0.13 (na[d])	0.52–0.52 (na)	0.17–0.21 (na)
Noxubee NWR, Miss.	37–211 (118)	0–92 (39)	26–88	na[b]	na	na
Piedmont NWR, Ga.	14–274 (149)	0–153 (72)	18–75	na[b]	na	na
Savannah River Site, S.C.	18–302 (146)	40–288 (129)	13–60	0.10–0.23 (0.13)	0.38–0.58 (0.44)	0.10–0.17 (0.13)

[a] NWR, National Wildlife Refuge.
[b] No CV calculated because data for individual animals were no longer available.
[c] WMA, Wildlife Management Area.
[d] No median because only 2 years of data for individual animals are available.
[e] LBL, Land Between the Lakes National Recreation Area.

pendent influences in white-tailed deer. We also are aware of deer herd managers who have used such averages to reduce annual variation in population parameters (K. Kammermeyer, personal communication).

We converted absolute densities derived from reconstruction to relative densities by dividing them by estimates of K specific to each population. This estimate is based on the value of K associated with stock-recruitment curves developed for each population by Keyser et al. (2005b) following the form:

$$\text{fawn density} = \text{yearling and adult female density} + (\text{yearling and adult female density})^3$$

after White and Bartmann (1997). This model can more precisely be restated as follows:

$$(\text{fawn density})_{\text{year } 0} = (\text{total adult density})_{\text{lag 2 years}} - [(\text{total adult density})_{\text{lag 2 years}}]^3$$

or

$$(AD\male_0 \times ASR_0 \times FDR_0) = [(AD\male_2 \times ASR_2) + AD\male_2] - [[(AD\male_2 \times ASR_2) + AD\male_2]^3,$$

where $AD\male_0$ = adult male density in year 0, ASR_0 = adult sex ratio in year 0, FDR_0 = fawn:doe ratio in year 0, $AD\male_2$ = adult male density year $T-2$, and ASR_2 = adult sex ratio year $T-2$.

These estimates of K and relative density are derived from population reconstruction and are population specific. As such, they are biased low because reconstruction estimates minimum densities (Downing 1980). However, because these estimates are population-specific, the biases within a given population for both K and annual densities should be consistent and, therefore, the estimates of relative density should not be biased low. Time dependency may be of concern, but this has been accounted for using the autoregressive models described below. Following McCullough (1979), we defined recruitment at 6 months of age.

We chose 4 physical parameters based on Keyser et al. (2005a) and their general use by herd managers throughout

the Southeast: number of antler points (POINTS), percentage spike-antlered yearling (SPIKE), and male and female field-dressed body mass measured in kilograms (MYM and FYM, respectively) for yearlings (17–19 months old). We used 2 antler measures because no one measure was available for all of the populations. All parameters were annual means collected from harvested deer. It should be noted that for 4 populations, data for individual deer are no longer available and, therefore, no measures of variability could be calculated for these parameters. Where data were still available, however, we computed coefficients of variation (Table 1).

We examined relationships using standard linear regression techniques (Neter et al. 1996) with relative density as the dependent variable and the physical parameters as independent variables. All models ($n = 18$) for which Keyser et al. (2005a) reported a significant relationship using absolute density as the response variable were reanalyzed using relative density. We only examined significant models because our purpose was not to determine whether or not a density–physical condition relationship existed but, rather, to assess relationships already known to exist in a new context: relative density. We evaluated residuals for all models to assess appropriateness and conformity to assumptions of normality and variance. Based on examination of residuals and the fact that Keyser et al. (2005a) found nonlinear models were not appropriate for density–physical condition relationships, we did not use nonlinear models. Because all data were drawn from time series and were based on 3-year running averages, we examined all models for autocorrelation using a Durbin–Watson test (Neter et al. 1996) and we utilized remedial models (Yule–Walker) where indicated (Harvey 1981, Neter et al. 1996, SAS Institute 1996). To account for autocorrelation of errors (SAS Proc AUTOREG; SAS Institute, Cary, North Carolina), final models were of an autoregressive form and were in full conformity to assumptions of normality and variance.

We compared POINTS, MYM, and FYM models among populations using an analysis of covariance model to test heterogeneity of slopes with populations as groups (SAS Institute 1996). Because this model did not control for experiment-wise error in between-population comparisons,

Table 2. Regression models for relative density (based on a 2-yr lag) versus male field-dressed body mass for 7 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998. Relative density (dependent) and mass (independent) variables are 3-yr running averages.

Population	n (yr)	Intercept	Slope[a]	Slope SE	r^2	P	D[b]
Crab Orchard, Ill.	13	4.0876	−0.0342 A[c]	0.0041	0.89	≤0.001	1.41
Fort Stewart, Ga.	9	1.9597	−0.0197	0.0062	0.63	0.019	1.96
Highland–Bath, Va.	27	3.4220	−0.0379	0.0084	0.45	≤0.001	0.32[d]
Land Between the Lakes, Ky.	20	2.5212	−0.0214 AB	0.0048	0.54	≤0.001	1.46
Noxubee, Miss.	14	3.8281	−0.0362 AB	0.0074	0.70	0.001	1.32
Piedmont, Ga.	23	2.3691	−0.0247 AB	0.0039	0.68	≤0.001	1.88
Savannah River, S.C.	27	1.2632	−0.0105	0.0050	0.16	0.046	1.12[d]

[a] All models, except Highland–Bath, are based on Yule–Walker estimates. Highland–Bath parameters are estimated by ordinary least-squares methods.

[b] Durbin–Watson D statistic.

[c] Analysis of covariance testing for heterogeneity of slopes. Neither Savannah River nor Highland–Bath populations were included in this analysis due to the presence of significant autocorrelation. Slopes followed by the same letter are not different ($P = 0.05$).

[d] Significant first-order autocorrelation ($P = 0.05$).

we used a Bonferroni technique with a test criterion of $P = 0.05$. We did not include models with significant autocorrelation in this comparison because they are likely to have overestimated slopes and underestimated standard errors (Neter et al. 1996). We did not compare POINTS models with SPIKE models because the parameters, units of measure, and the nature of the relationship (positive vs. negative slopes) were different.

We ranked populations with significant MYM models by 2 presumed measures of overall habitat productivity: per capita rate of increase (r), and maximum observed mass. Based on ordination of the populations using these 2 variables, we compared slopes for the 4 types of models (MYM, FYM, SPIKE, and POINTS) to assess the possible influence of habitat quality on slope.

Results

Relative densities computed for the 8 populations ranged from 10% to 100% and varied by a factor of 2.0–5.4 within populations (Table 1). A qualitative assessment of within-population trends in relative density indicated a pattern of increase followed by increased harvest and subsequent reductions in relative density. Typically each population repeated this cycle 2–3 times during the study period. Physical condition measures had consistently low coefficients of variation during the study period (Table 1).

Using relative density, we reanalyzed the 7 MYM models (Keyser et al. 2005a) that had significant relationships. Simple linear transformation of the response variable had a negligible effect on model strength as seen in coefficients of determination (Table 2). Models explained between 16% and 89% of the variability in relative density with 6 explaining >45%. With the exception of HB, all models were of an autoregressive form to accommodate autocorrelation, and only one of those (SR) failed to correct it. Comparison of slopes revealed that only FS (−0.0197) was different from CO (−0.0342) among the 5 MYM models tested using a conservative approach (Bonferroni with $P = 0.05$). Slope estimates for these 5 ranged from −0.0197 to −0.0362 (Table 2).

We reanalyzed 6 antler models, 4 using POINTS and 2 (CO and HB) using SPIKE, for which Keyser et al (2005a) reported significant relationships. As was the case with the 7 MYM models, the linear transformation of the response variable had a negligible effect on model strength as seen in coefficients of determination (Table 3). Antler models explained less of the variation in relative density (0.34–0.65) than the MYM models but were more consistent with respect to r^2 values with 5 between 0.34 and 0.46 (Table 3). As was the case with MYM models, both HB (least-squares model) and SR (autoregressive model) had significant autocorrelation. Because of this and the fact that the CO

Table 3. Regression models for relative density (based on a 2-yr lag) versus antler measures[a] for 6 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998. Relative density (dependent) and antler (independent) variables are 3-yr running averages.

Population	n (yr)	Intercept	Slope[b]	Slope SE	r^2	P	D[c]
Crab Orchard, Ill.	13	1.2065	−0.0097	0.0024	0.65	0.003	1.65
Highland–Bath, Va.	27	0.7266	−0.0114	0.0025	0.46	≤0.001	0.36[d]
Land Between the Lakes, Ky.	17	1.0197	−0.1406 A[e]	0.0440	0.44	0.007	1.74
Noxubee, Miss.	15	2.0742	−0.4557 A	0.1810	0.37	0.029	1.33
Piedmont, Ga.	23	0.9630	−0.1696 A	0.0422	0.46	0.001	1.54
Savannah River, S.C.	27	1.3493	−0.2310	0.0657	0.34	0.002	1.19[d]

[a] Total antler points was used for all data sets except Crab Orchard and Highland–Bath, which used spike rate. In all cases the measure with the strongest correlation with density for that population was used.

[b] All models except Highland–Bath are based on Yule–Walker estimates. Highland–Bath parameters are estimated by ordinary least-squares methods.

[c] Durbin–Watson D statistic.

[d] Significant first-order autocorrelation ($P = 0.05$).

[e] Analysis of covariance testing for heterogeneity of slopes. Neither Savannah River nor Highland–Bath were included in this analysis due to the presence of significant autocorrelation. Slopes followed by the same letter are not different ($P = 0.05$). Crab Orchard, the only other SPIKE model, was also not included in the comparisons with POINTS models.

Table 4. Regression models for relative density (based on a 2-yr lag) versus female field-dressed body mass for 5 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998. Relative density (dependent) and mass (independent) variables are 3-yr running averages.

Population	*n* (yr)	Intercept	Slope	Slope SE	r^2	*P*	*D*[a]
Crab Orchard, Ill.	13	3.7655	−0.0375 AB[b]	0.0111	0.56	0.008	1.23
Fort Stewart, Ga.	9	1.8540	−0.0211 B	0.0093	0.51	0.072	0.88[c]
Lake Russell, Ga.	18	1.1194	−0.0108	0.0054	0.21	0.063	1.03[c]
Noxubee, Miss.	14	4.6712	−0.0558 A	0.0124	0.67	0.001	1.54
Piedmont, Ga.	23	2.3475	−0.0278 B	0.0048	0.64	≤0.001	2.05

[a] Durbin-Watson *D* statistic.
[b] Analysis of covariance testing for heterogeneity of slopes. Lake Russell was not included in this analysis because of significant autocorrelation. Fort Stewart was included because the autocorrelation was marginal ($P = 0.04$). Slopes followed by the same letter are not different ($P = 0.05$).
[c] Significant first-order autocorrelation ($P = 0.05$).

antler model was for SPIKE, only 3 slopes could be compared (LBL, NX, PM) and they were not different ($P < 0.05$).

We used 5 FYM models developed by Keyser et al (2005*a*) with a significant relationship versus absolute density in our relative density analysis and observed no change in *P*-values (all models that had been significant remained so) and coefficients of determination (Table 4). Our models explained 21–67% of the variation in relative density with 4 explaining >51%. We used autoregressive error models for all 5 populations, but for 2 of those (FS and LR) the autocorrelation was not corrected (Table 4). Based on our comparison of slopes, only NX (−0.0558) was different ($P > 0.05$) from FS (−0.0093) and PM (−0.0048).

Model parameters changed under relative density compared to absolute density (Keyser et al. 2005*a*), as did the rank order among populations with respect to slope (Table 5). Rank order for POINTS models did not change for the 3 populations that were tested. Changes in rank order for both MYM and FYM models were the result of NX moving from third place to first place.

Per capita rate of increase (r) and maximum observed mass gave a generally consistent ordination of the populations (Table 6). Though, when this ordination was compared to ranks for slopes of MYM, FYM, and antler models, it did not seem habitat quality alone was a consistent factor in understanding variation in slopes (Table 6). Another comparison of slopes and parameters among populations is the ratio of antler slope and FYM slope to the MYM slope (Table 6). In SR

antlers changed much more slowly with relative density than MYM (21:1), but for LBL the 2 variables changed at a more comparable rate (6.7:1). Female field-dressed body mass, on the other hand, has a ratio that remains between 1.1 and 1.6 for the 4 populations represented, indicating that the 2 variables track well together.

Discussion

Absolute density has been shown to influence physical condition in white-tailed deer (Johnson 1937, Clutton-Brock et al. 1982, Leberg and Smith 1993, Keyser et al. 2005*a*). However, no previous study has quantified the relationship between physical condition and relative density. McCullough (1984) recognized such a relationship and described changes as they related to male mass and antler configuration, but stopped short of defining the relationship in discrete, quantitative terms. He generally dealt with relative densities as they related to recruitment. Downing and Guynn (1985) also discussed relative density, but they examined it in the context of various reproductive and age-structure parameters. Jacobson (1992) established significant relationships between female harvests in the preceding 2 years and 1.5- and 2.5+-year-old male body mass, antler beam length, and antler circumference, but not for female body mass. The implications of female harvest for density are obvious, but nevertheless, density was not estimated in his study.

Although not examining relative density explicitly, Severinghaus and Moen (1983) derived useful predictive

Table 5. Rank order of slopes for male (MYM) and female (FYM) field-dressed body mass and antler models using relative density and absolute density (Keyser et al. 2005*a*) models for 8 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998.

	MYM		Antler[a]		FYM	
Population	Absolute density rank (slope)	Relative density[b] rank (slope)	Absolute density rank (slope)	Relative density rank (slope)	Absolute density rank (slope)	Relative density rank (slope)
Crab Orchard, Ill.	1 (−3.393)	2 (−0.034)	(−1.015)	(−0.010)	1 (−3.946)	2 (−0.038)
Fort Stewart, Ga.	5 (−0.120)	5 (−0.020)	na[d]	na	4 (−0.129)	4 (−0.021)
Highland–Bath, Va.[c]	(−3.952)	(−0.038)	(−1.193)	(−0.011)	na	na
Lake Russell, Ga.[c]	na	na	na	na	(−0.802)	(−0.011)
Land Between the Lakes, Ky.	4 (−1.067)	4 (−0.021)	3 (−7.017)	3 (−0.141)	na	na
Noxubee, Miss.	3 (−1.110)	1 (−0.036)	1 (−13.990)	1 (−0.456)	3 (−1.713)	1 (−0.056)
Piedmont, Ga.	2 (−1.680)	3 (−0.025)	2 (−11.547)	2 (−0.170)	2 (−1.891)	3 (−0.028)
Savannah River, S.C.[c]	(−0.245)	(−0.011)	(−5.383)	(−0.231)	na	na

[a] Total antler points was used for all data sets except Crab Orchard and Highland–Bath, which used spike rate. In all cases the measure with the strongest correlation with density for that population was used.
[b] Relative density = total adult density/K-carrying capacity based on third-order recruitment models.
[c] Population not included in rankings due to presence of significant autocorrelation.
[d] na = not applicable.

Table 6. Some comparisons among 7 white-tailed deer populations in the midwestern and southeastern United States, 1967–1998.

Population	Per capita rate of increase[a]	Max. observed mass (kg)	Slope for relative density[b] models			Slope ratio	
			MYM[c]	Antler[d]	FYM[c]	Antler/MYM	FYM/MYM
Noxubee, Miss.	0.90	42	−0.036	−0.456	−0.056	12.67	1.56
Crab Orchard, Ill.	0.83	50	−0.034	−0.010	−0.038	0.29	1.12
Land Between the Lakes, Ky.	0.80	46	−0.021	−0.141	na[e]	6.71	na
Piedmont, Ga.	0.73	39	−0.025	−0.170	−0.028	6.80	1.12
Savannah River Site, S.C.	0.65	42	−0.011	−0.231	na	21.00	na
Fort Stewart, Ga.	0.62	34	−0.020	na	−0.021	na	1.05
Highland–Bath, Va.	0.54	41	−0.038	−0.011	na	0.29	na

[a] Per capita rate of increase = predicted fawn density/total adult density.
[b] Relative density = total adult density/K-carrying capacity.
[c] Male (MYM) and female (FYM) field-dressed body mass.
[d] Total antler points was used for all data sets except Crab Orchard and Highland–Bath, which used spike rate.
[e] na = not applicable.

relationships between antler beam diameter in yearling males and the number of embryos per yearling female. Against the backdrop of density-dependent recruitment patterns for white-tailed deer, it is clear they were evaluating a relationship between density and physical condition, though they discussed it in terms of range conditions. Because various density-independent factors affect range condition, the actual contribution of density in their analysis would be confounded to some degree.

We found that physical parameters can be useful indicators of relative density. This is particularly true of male yearling mass, and to a lesser degree, antler configuration for this same age class. All 3 physical indicators we analyzed tracked well for some populations suggesting that although slopes may vary somewhat, all 3 measurements (MYM, FYM, and antlers) can be used together to evaluate relative density.

The value of such relationships is more pronounced when biases that affect absolute density estimates and, in turn, the accuracy of such estimates, are considered. Indeed, whatever biases that may have been associated with reporting rates, recovery rates, or nonhunting mortality (all of which are important for population reconstruction) in each population likely would have canceled themselves out through conversion to relative density. Thus, if a particular population estimate was biased low, the estimate of K would also be low, but the relationship between the 2 estimates would remain consistent allowing for acceptable estimates of relative density. In any case the same technique was used for all populations, thus reducing bias potentially introduced by other methods. Furthermore, the relative density–physical condition relationships that we found appear consistent enough across populations for application to other herds in the southeastern United States without having to estimate absolute density and develop new models.

Although slopes estimated for each predictor varied, the magnitude of those differences was not great across the range of habitats and herd conditions examined. This suggests managers dealing with most herds in the Southeast can feel confident using these relationships as basic guidelines. It is worth noting that variability among antler characteristics is greater than for body mass as indicated by the ratios of slopes of the relationships. That this ratio differs from unity is explained by the fact that different units of measure were used in the predictors. That the magnitude of these ratios

varies as much as it does among populations suggests that the sensitivity of antler characteristics to relative density is dynamic. Thus, more caution is warranted in interpolating between populations with respect to antler measures than for mass. Similarly, using mass for females in other populations should be done with caution. Ordination of slopes along a presumed habitat-quality gradient did not provide convincing evidence that habitat quality was a satisfactory explanation for the observed differences. Thus, developing a "family" of habitat-quality equations was not justified. The steeper slopes (CO, HB, and NX) indicate that larger changes in density are associated with each unit change in mass. Or from a biological perspective, body mass is less sensitive to changes in relative density for these populations.

This could be explained by a variety of factors. For CO abundant food resources may have a buffering effect on changes in relative density and, therefore, small changes in relative density do not show up quickly in body mass. For HB periodic mast crops may serve this same role, albeit less consistently. A second possible influence for HB may be relative herd density, which has been high for many years. Mass seems to vary less at high densities than at lower relative densities. This also may be true for the NX herd because it, too, had relative densities above 50% of K for nearly the entire analysis period and, as such, may not have exhibited its full range of body masses and mass–density responses. Finally, it is possible that varying slopes may be genetically determined. McCullough (1982) found that differences in antler characteristics for local populations were more apparent than for regional populations and suggested this may be due to local hereditary patterns. We found high between-population variability in the relative sensitivity of antler measures that support this conclusion.

Because the relationships for physical indices we examined were linear, there is no readily apparent identifier of the inflection point in the stock-recruitment functions that we developed. This is not a problem for the populations we examined because physical indices were associated with a specific relative density. Not only could a change in the magnitude of relative density be discernable, but the actual point on the curve could be determined. For herds where data are not available to allow for calibration, only the magnitude of change can be determined with some precision. Because of the limitations of data available for

this study, it was not possible to identify age-specific fecundity rates that might allow for identification of benchmark FDR or other measures associated with this inflection point. Where fawn breeding rates or yearling breeding rates can be measured, these likely will prove useful in this regard (McCullough 1979, Downing and Guynn 1985). Also, if some threshold body mass can be consistently related to fawn breeding rates, it could be a valuable surrogate (Harder 1980).

A fundamental assumption to our approach is that stock-recruitment curves are a reliable context in which to understand white-tailed deer population responses to management actions affecting relative density. McCullough (1979) found that 2 experiments with white-tailed deer at the George Reserve in Michigan separated by 40 years showed similar results in terms of estimates of carrying capacity and rate of population increase. There have been cases of irruptive population behavior in ungulates (McCullough 1997), but the circumstances hypothesized as causing them do not appear operative in the populations we studied. We believe most environments across the region we examined were relatively stable and did not lend themselves to wide variations in biotic factors likely to dramatically alter carrying capacity (see Miller and Wentworth 2000) and, by inference, the stock-recruitment curves that appear to characterize these populations.

Management Implications

While managers have subjectively used mass and antler measures as indicators of deer herd health, we believe more precise application of these data to actual herd conditions is possible. For instance, it will be possible to know with reasonable confidence if management strategies have increased or decreased relative density in increments as small as 2–4% of K. Furthermore, despite substantial differences in absolute measures of mass, implications of changes in mass are consistent: a 0.4-kg change in yearling male body mass represents a change in relative density of between 1.1–3.8% for these populations. This consistency across a wide range of habitats tends to support the concept that this is a universal relationship modified by various local influences.

Unfortunately, it will not always be clear at what segment of the curve change has occurred. For the populations we examined, we were able to calibrate relative densities with a defined stock-recruitment curve; they can be used to identify position of the herd with respect to important thresholds such as the inflection point (I-carrying capacity). Most local

deer herds (i.e., property-level management), because of the small size of the annual harvest on such areas, are unlikely to generate enough harvest data to enable derivation of a productivity curve with any degree of confidence, making such a calibration impossible. Managers must then rely either on models such as those we developed or other evidence to surmise relative position of a herd on the curve.

With only 2 exceptions, populations we evaluated did not exceed the inflection point of the stock-recruitment curve by any appreciable degree. Considering that these populations were managed for a median duration of 26 years during which most populations were repeatedly increased to some threshold and then reduced by more liberal harvest regulations, it seems reasonable to assume deer densities in these habitats exceed society's tolerance at a level that is at or below I-carrying capacity. Therefore, it would not be unreasonable for a manager to begin with the presupposition that a herd is likely to be on the left leg of the curve and then seek evidence to the contrary.

Managers will certainly benefit by using all 3 parameters (MYM, FYM, and antlers) together when assessing a deer herd. Reliance on either antler measures or FYM alone would not be prudent because antler configuration was a less consistent measure than MYM, and FYM was not significant for 3 of the 8 populations examined. It also is important to recognize that not all populations responded to changes in density. On poorer habitats, density-independent factors may be of much greater consequence, and the utility of the models we developed, or similar ones, will be minimal.

Acknowledgments

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Associate Editor: Whittaker.