

Influence of Time Lags and Population Segment in Density-physical Parameter Relationships in White-tailed Deer

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Abstract: Managers and biologists have long relied on relatively inexpensive and easily collected data from hunter-harvested deer to provide information for making harvest management decisions. We sought to better understand the influence of time lags and population segment (i.e., total adult and total herd density) on the density-physical parameter relationship. Nine long-term harvest data sets (15–31 years duration, median = 26 years) were acquired from populations located across the Southeastern United States which spanned several physiographic provinces and a wide range of densities (1–32 deer/km²). Population densities were derived from a combination of Downing and Wisconsin reconstructions. These densities were correlated to commonly used physical parameters in the current year and with one- and two-year lags. Time lags proved to be useful in identifying the relationship between physical parameters and density for both the total and adult segments of the herd. The one-year lag was useful, but the two-year lag had nearly twice as many populations demonstrating a significant ($P < 0.05$) relationship with density compared to the current year. Population segment also was important in identifying relationships. In all cases, more populations exhibited significant relationships when examined in the context of adult rather than total herd density. We suggest that the appropriate context for understanding density-physical parameter relationship in white-tailed deer is lagged adult densities. These results also offer support to the argument that *Odocoileus* populations operate in a density-dependent manner.

Key words: density, physical condition, time lags, mass, white-tailed deer

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The combination of the white-tailed deer's (*Odocoileus virginianus*) popularity as a game animal and the substantial economic losses associated with this species has placed increasing emphasis on population management. This, in turn, will require management prescriptions and density adjustments based on sound population esti-

mates. Some traditional population estimation techniques such as track counts, pellet group counts, spotlight counts, change-in-ratio estimators, and strip censuses have met with limited success. More elaborate methods used in recent years (e.g., mark-recapture and line-transect models) require investments of time and money that can be substantial. A number of condition indices (i.e., blood parameters, organ mass) require expensive equipment or laboratory analysis. Furthermore, these indices can be sensitive to seasonal and environmental factors, especially those which affect deer diet and nutrition (Warren et al. 1981, Sams et al. 1998), and which, in turn, may or may not directly relate to deer density. These indices may require special collection of specimens during times other than hunting season. Clearly, hunter-killed deer are a far less expensive and more convenient source of data.

Roseberry and Woolf (1991) explored a number of population estimation techniques that relied on existing harvest data. They reported that population reconstruction and Catch Per Unit Effort (CPUE) were the best among the population monitoring methods they examined when considered from the perspective of accuracy, precision, sensitivity and robustness. Because CPUE methods require input of effort data, they can be used in only limited circumstances.

To make the best use of physical data from hunter harvested deer (e.g., antler dimensions and body mass), it is important to have a clear understanding of how these data relate to deer density. The population density-physical parameter relationship, in turn, may be influenced by two factors: time lags and the segment of the herd being considered (Clutton-Brock et al. 1982, Leberg and Smith 1993). Several studies have examined how environmental conditions such as precipitation (Teer et al. 1965, Feldhamer et al. 1989, Ginnett and Young 2000) and acorn crops (Feldhamer et al. 1989, Osborne et al. 1992, Wentworth et al. 1992) affect physical condition of deer in subsequent years. These workers identified lagged responses including changing body mass, density, fawn:doe ratios, and recruitment. They attributed these various changes to improved range quality resulting from increased rainfall or mast crop. Jacobson (1992) documented that body mass and antlers for 1.5-year-old deer responded two years after a change in antlerless deer harvest levels. These studies suggest that time lags may be an important consideration in the dynamics of white-tailed deer herds. Although various studies have suggested that segregation of sexes in cervids can be important biologically (Clutton-Brock et al. 1982, Miller and Ozoga 1997), no one to our knowledge has linked this quantitatively to variation in physical condition as a function of density. Thus a lack of direct competition between fawns and adults for resources, and the influence of the time lags described above, may mean that fawns do not appreciably contribute to density-physical condition relationships.

We hypothesized that the segment of the population (i.e., total herd versus adult density only) may be a very important consideration in further developing relationships between physical condition and herd density. We also hypothesized that one- and two-year time lags would be the preferred context for understanding these relationships for fawns and 1.5-year-olds, respectively. Our objective, therefore, was to relate various physical parameters (i.e., antler dimensions and body mass) to reconstructed herd density estimates using total herd and adult-only densities in the current

Table 1. Some attributes of populations used to examine density-dependent responses in white-tailed deer population management.

Population		Area (km ²)	Duration (years)	Mean harvest (deer/year)	Density ^a range (deer/km ²)	Physiographic province
Fort Bragg, North Carolina	(FB)	497	15	877	6–10	CP ^b (Sand Hills)
Crab Orchard NWR ^c , Illinois	(CO)	73	25	616	13–32	Loess Drift
Fort Stewart, Georgia	(FS)	940	15	265	<4	CP (Coastal Flat Woods)
Highland-Bath counties, Virginia	(HB)	2227	31	5,242 ^d	4–22	Ridge and Valley
Lake Russell WMA, Georgia	(LR)	70	23	278	5–15	Piedmont (upper)
LBL - Kentucky section only	(LBL)	399	26	959	8–21	Interior Low Plateau
Noxubee NWR, Mississippi	(NX)	179	26	378	3–10	CP (Interior Flat Woods)
Piedmont NWR, Georgia	(PM)	153	31	626	5–20	Piedmont
Savannah River Site, South Carolina	(SR)	803	31	1,036	1–5	CP (Upper)

a. Total adult density (>1.5 years old).

b. Coastal Plain.

c. National Wildlife Refuge.

d. Total reported harvest. Data collected on an average of 765 animals per year. For all other populations, samples were taken on nearly 100% of reported harvest.

year, the preceding year, and two years earlier. We examined these relationships to determine if useful density-dependent relationships existed, and in the event that they did, identify the most appropriate context for evaluating density-physical parameter relationships using populations from several physiographic provinces in the Southeastern United States.

Methods

We examined nine study populations, eight from several physiographic regions in the Southeast and one from the Midwest (Table 1). Criteria for selection of data sets included a minimum of seven continuous years of data, an average annual harvest of at least 100 animals, data collected from harvests on a contiguous land area, age structure available through the 2.5-year age class, and traditional deer harvest strategies that had not selected against males with smaller antlers (i.e., quality deer management). All nine study populations met or exceeded these criteria.

Using data from hunter-harvested deer, we developed population estimates based on standard reconstruction techniques (Downing 1980). We used this technique to estimate antlered male populations using two age classes (ages 1.5 and 2.5 years). We estimated female and fawn numbers by a Wisconsin reconstruction (Creed et al. 1984, Roseberry and Woolf 1991). We converted population sizes to densities (deer/square kilometer) based on property size. For the purposes of this analysis, we defined two population segments: total herd, which included fawns, sub-adult (1.5 years old), and adult (2.5+ years old) males and females; and adult herd,

which included only sub-adult and adult males and females. We computed two estimates of density: one for the total adult segment of the herd and one for the total herd.

We chose four physical parameters for this study: mean number of antler points (POINTS) or percent spike-antlers (SPIKE) for yearling males (17–19 months old), mean yearling male field-dressed body mass (BYM), and mean male (BFM) and female (DFM) fawn field-dressed body mass. All parameters used in these analyses were annual means collected from harvested deer. We selected these four variables based on their use by herd managers throughout the Southeast. Because available measures of yearling male antler development were inconsistent among populations, we chose those most widely available and with the consistently strongest relationship to density. This resulted in mean number of points being used for most populations and spike rate being used for the others.

We correlated total herd density and adult density for the current year to POINTS, SPIKE, BYM, BFM, and DFM. We lagged both densities one and two years and correlated them to physical parameters for yearlings. We correlated fawn mass to both densities in the current year and lagged one year only. We evaluated all relationships using PROC CORR (SAS 1993) for Pearson correlations (Neter et al. 1996) with a rejection criterion of $P < 0.05$. Because all comparisons were made within populations rather than between populations, autocorrelation was not deemed to be a significant concern and was not evaluated.

Results

These long-term data sets are drawn from populations on large properties that cover a wide range of habitat conditions and density ranges (Table 1). A brief profile of data sets and data quality is presented in Table 2. For a number of populations, data for individual deer were no longer available and, therefore, no measures of variability are presented. Thus Table 2 presents coefficients of variation (CV) for only four populations. Variances for physical data, particularly yearling body mass, remained stable across years and populations. Large sample sizes were available for population reconstruction (Table 2).

For mean annual field-dressed body mass for 1.5-year-old males, we observed significant relationships for seven of nine populations (Table 3). Antler measures for 1.5-year-old males were significantly correlated with at least one density estimate for six of nine populations (Table 3). For the Crab Orchard and Highland-Bath populations, spike rate was used as the antler measure and, thus, the correlations are positive rather than negative as was the case with the four populations with significant relationships for POINTS. Only Crab Orchard and Fort Stewart had significant correlations for male fawn mass ($r = -0.67$, $P = 0.01$, and $r = -0.76$, $P = 0.01$, respectively for one-year lag) and only Fort Stewart and Savannah River Site had them for female fawn mass ($r = -0.81$, $P < 0.01$, and $r = -0.57$, $P < 0.01$, respectively for one-year lag). We did not observe any significant correlations for fawn mass in the current year.

Across all nine populations, we observed significant correlations more fre-

Table 2. Sample sizes (annual) and variability of data, expressed as coefficients of variation (CV), for nine white-tailed deer populations used in analysis.

Population	<i>N</i> yearling males range (mean)	<i>N</i> yearling females range (mean)	Coefficients of Variation (CV)			
			Yearling male mass range (median)	Yearling male antler points range (median)	Fawn male mass range (median)	Fawn female mass range (median)
FB ^a	135–375 (257)	45–107 (72)	na ^b	na	na	na
CO	45–213 (140)	42–136 (69)	na	na	na	na
FS	18–97 (53)	5–40 (17)	na	na	na	na
HB	49–350 (163)	11–161 (64)	0.14–0.18 (0.16)	0.43–0.50 (0.47)	0.14–0.19 (0.18)	0.16–0.24 (0.18)
LR	48–143 (93)	5–46 (23)	0.15–0.16 (c)	0.34–0.35 (c)	0.15–0.22 (c)	0.16–0.16 (c)
LBL	120–410 (260)	8–232 (76)	0.12–0.13 (c)	0.52–0.52 (c)	0.20–0.22 (c)	0.19–0.20 (c)
NX	37–211 (118)	0–92 (39)	na	na	na	na
PM	14–274 (149)	0–153 (72)	na	na	na	na
SR	18–302 (146)	40–288 (129)	0.10–0.23 (0.13)	0.38–0.58 (0.44)	0.13–0.36 (0.19)	0.13–0.37 (0.18)

a. Abbreviations for study populations follow Table 1.

b. Not available.

c. No median since only two years of data for individual animals are available.

quently between yearling physical parameters (BYM, SPIKE, and POINTS) and adult densities than between those same parameters and total density (Table 4). One- and particularly two-year lags produced more significant relationships than did current-year densities (Table 4). The same pattern also was observed for fawn mass, with adult density and time lags (one-year) providing the best correlations.

For each physical parameter, the density estimate that provided the strongest significant correlation for each population was identified. For BYM, the two-year lag proved to be the strongest relationship in five of seven instances (Table 3). In all seven populations with significant relationships for BYM, adult density provided a stronger correlation (i.e., higher *r*) than total density. Antler measures showed the same pattern with only Noxubee NWR (current year) and Highland-Bath (one year lag) not being strongest with the two-year lag, and only Piedmont NWR not having the strongest relationship for adult density. In the latter case, however, the difference was minimal (*r* = 0.67 vs. 0.66). For three populations (Fort Stewart, Land Between the Lakes, and Savannah River Site), the two-year lag for adult density was the only significant correlation for yearling mass. For two of those populations (Land Between the Lakes and Savannah River Site), the two-year lag was the only significant correlation for antler measures. For fawn mass, correlations were strongest in all four cases with adult density lagged one year.

Table 3. Pearson correlation coefficients (r) between yearling male mass and antler measures^a and three density measures of white-tailed deer populations.

Population	Yearling male mass					
	Current year		One-year lag		Two-year lag	
	r	$P <$	r	$P <$	r	$P <$
FB ^b	0.53	0.07	-0.02	0.95	0.25	0.40
CO	-0.40	0.11	-0.66	0.01	-0.80	0.001
FS	-0.22	0.49	-0.50	0.10	-0.61	0.03
HB	-0.65	0.001	-0.61	0.001	-0.45	0.02
LR	-0.01	0.98	-0.17	0.47	-0.30	0.20
LBL	0.02	0.93	-0.37	0.08	-0.49	0.02
NX	-0.59	0.001	-0.55	0.01	-0.65	0.001
PM	-0.64	0.001	-0.64	0.001	-0.54	0.001
SR	-0.19	0.32	-0.16	0.39	-0.36	0.05

Population	Antler measures					
	Current year		One-year lag		Two-year lag	
	r	$P <$	r	$P <$	r	$P <$
FB ^b	0.23	0.50	-0.13	0.70	0.14	0.66
CO	0.39	0.13	0.63	0.01	0.67	0.01
FS	-0.39	0.21	0.15	0.65	-0.17	0.59
HB	0.38	0.04	0.49	0.01	0.45	0.02
LR	-0.14	0.56	0.00	1.00	-0.09	0.70
LBL	0.05	0.85	-0.26	0.26	-0.50	0.02
NX	-0.55	0.01	-0.39	0.09	-0.47	0.04
PM	-0.38	0.07	-0.58	0.001	-0.66	0.001
SR	-0.10	0.60	-0.31	0.11	-0.42	0.02

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. Abbreviations for study populations follow Table 1.

Discussion

Many studies of deer have underscored the impact of diet on both body mass and antler development (Abler et al. 1976, Verme and Ozoga 1980, Ozoga and Verme 1982). The influence of nutrition on development begins at conception and can be seen in fawn birth mass and survival (Verme 1965, Verme 1969, Clutton-Brock et al. 1982). Fawn development through the first summer is also affected by nutrition (Abler et al. 1976, Verme and Ozoga 1980). Growth continues relatively rapidly through about 1.5 years and then slows appreciably (Leberg and Smith 1993, Strickland and Demarais 2000). Hence, it seems apparent that nutrition from conception through age 1.5 would influence physical condition at any point during that time. Further, because growth is much less pronounced after age 1.5, it stands to reason that the influence of nutrition on physical condition would be less obvious. This val-

Table 4. Number of significant correlations ($P < 0.05$) by population segment and time period for white-tailed deer.

Parameter	Total density			Adult density			Populations assessed
	Current year	One-year lag	Two-year lag	Current year	One-year lag	Two-year lag	
Yearling male							
Mass	2	3	4	3	4	7	9
Antlers ^a	0	2	4	2	3	6	9
Subtotal	2	5	8	5	7	13	
Fawn mass							
Males	0	0	b	1	2	b	8
Females	0	1	b	0	2	b	8
Subtotal	0	1	b	1	4		

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. Not available.

idates the use of 0.5- and 1.5-year age classes in assessing density and/or nutritional status in a herd. It also suggests one possible explanation for the efficacy of lags in understanding the relationship between density and physical condition.

Another likely explanation is the influence of changing range conditions on herd condition. Studies have shown that both acorn crops (Wentworth et al. 1992) and rainfall (Teer et al. 1965, Feldhamer et al. 1989) impact deer condition through alterations of range quality. In any case, for seven of the nine populations examined here, it is apparent that the time lag is an important aspect of the density-physical condition relationship, and in several cases was critical to identifying the correlation. Furthermore, the time lag strengthens the correlations, thus making the development of predictive models much more likely.

Consistent with our results, Leberg and Smith (1993) concluded that adult densities were more useful in explaining changes in physical parameters than were total herd densities. They thought that the explanation for this was largely sociobiological in nature, being based on increased breeding competition among males. If this is the case, certainly fawns represent no competition for breeding privileges to adult males. Also, fawns are not likely to represent much competition to adults, particularly males, for food because they remain with their mothers through their first year of life. Differential habitat use by males and females (McCullough 1979) also may mean that male physical measures are not related to direct competition with fawns, because fawns are segregated from older males. Verme (1991) hypothesized that female fawns were largely suppressed in terms of breeding activity by presence of their mothers. This suggests a subordinate role of fawns in the social context of a herd, something that Miller and Ozoga (1997) also described for male fawns. Thus total herd density, which includes fawns, masks the social competition resulting from density-driven competition among adults. As with lags, looking at adult density allowed

the identification of three populations where physical-density relationships were significant and would not have otherwise been detected.

Despite the large number of significant relationships that we identified, two populations did not demonstrate any apparent density-dependent responses. Other studies have failed to link density and physical parameters on marginal ranges (Osborne et al. 1992, Shea et al. 1992), leading many biologists to conclude that some habitats are simply too poor to enable density-dependent responses to either be detected or to occur (Shea and Osborne 1995). The basic hypothesis of these authors is that in the absence of either elevated rainfall or mast, baseline levels of nutrition are simply too poor to allow for any alteration in either herd dynamics or condition. It may be that the habitat at Fort Bragg is of such low quality that such a pattern would be expected (Shea and Osborne 1995).

In this analysis, we do not attempt to develop any predictive models. Rather we are simply creating the framework in which to define more precise hypotheses to develop those models. The populations examined in this study provided long-duration data that undoubtedly captured a great deal of stochasticity resulting from density-independent factors. Despite any impact from these factors, significant relationships were detected for density in seven of nine populations. These results suggest that density-dependent processes are the dominant influence in herd dynamics in the Southeastern United States and that other forces, which are often outside of the control of managers, tend to modulate the impact of density.

Management Implications

Managers of white-tailed deer herds in the Southeastern United States and elsewhere have relied on physical condition as an easily measured surrogate for herd density. This study provides justification for continuing this practice but especially with a focus on BYM, and to a lesser degree antler configuration (SPIKE and/or POINTS) for the same age class. Antler measures should be used to supplement, but not in preference to, body mass when assessing herd condition.

However, several precautions should be taken in applying these condition indices. First, managers working with herds on very poor ranges will not likely see responses. Secondly, where quality deer management is being practiced, and yearling males are not being harvested in adequate numbers to provide meaningful sample sizes, other indices must be sought. Our work suggests that fawn weights will not generally be a satisfactory substitute. Thirdly, although we observed strong correlations in response to wide variations in density, assessing whether these relationships were linear or non-linear in nature was beyond the scope of this study. At some upper or lower density extremes, there may be thresholds above or below which the relationships change. However, we believe that the relationships will be valid across the range of densities observed for our populations. Thus, for most populations even modest changes in absolute density, such as were seen at Savannah River Site, should result in measurable changes in body condition.

Finally, managers should recognize that condition indices do not respond imme-

diately to changing densities. Deer herds require two years to reflect such changes and, therefore, results from management actions may also be delayed by that same time period. Making adjustments to harvest plans prematurely can lead to undesired consequences.

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