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SENSITIVITY OF CONDITION INDICES TO CHANGING DENSITY IN A WHITE-TAILED DEER POPULATION

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ABSTRACT: The ways in which comprehensive condition profiles, incorporating morphometric, histologic, physiologic, and diet quality indices, responded to changes in density of a white-tailed deer (*Odocoileus virginianus*) population were examined. Changes in these condition indices were monitored in a northeastern Oklahoma deer herd as density declined from peaks of 80 and 72 deer/km^2 in 1989 and 1990 (high-density) to lows of 39 and 41 deer/km^2 in 1991 and 1992 (reduced-density), respectively. Compared to a reference population (6 deer/km^2), deer sampled during high-density exhibited classic signs of nutritional stress such as low body and visceral organ masses (except elevated adrenal gland mass), low fecal nitrogen levels, reduced concentrations of serum albumin, elevated serum creatinine concentrations, and a high prevalence of parasitic infections. Although density declined by one half over the 4-yr study, gross indices of condition (in particular body mass and size) remained largely unchanged. However, selected organ masses, serum albumin and non-protein nitrogen constituents, and fecal nitrogen indices reflected improvements in nutritional status with reductions in density. Many commonly used indices of deer condition (fat reserves, hematocrit, total serum protein, and blood urea nitrogen) were not responsive to fluctuations in density.

Key words: Density, histology, nutritional condition, *Odocoileus virginianus*, organ mass, overpopulation, physiology, white-tailed deer.

INTRODUCTION

Understanding the relationship between density and environment is essential for successful management of white-tailed deer (*Odocoileus virginianus*) herds (Watkins et al., 1991). Numerous techniques have been developed for assessing these relationships using indices of animal condition or nutritional quality of their range. Among indices of animal condition, morphometric traits of white-tailed deer have been the most widely used (Severinghaus, 1955; McCullough, 1979); however, such indicators typically experience a time lag before responding to a change in density (Fryxell et al., 1991; Jacobson, 1992). Additionally, body mass is usually not sensitive to subtle changes in condition and does not accurately reflect specific nutrient deficiencies. Alternative approaches such as measures of organ mass (Ozoga and Verme, 1978; Verme and Ozoga, 1980a, 1980b), fat reserves (Ransom, 1965; Kistner, 1980), and metabolic status (Seal et al., 1978; Warren et al., 1981) have been recommended for improving diagnostic sensitivity. These alternative approaches have been promising, but their ability to detect changes in animal condition associated with changes in herd density in the wild has not been fully evaluated.

Collectively, the many studies on the use of condition indices in deer indicate that no single parameter can provide an accurate assessment of condition. Rather, profiles incorporating multiple indices appear to be necessary to fully characterize the condition of animals (Lochmiller et al., 1985; DelGuidice et al., 1990). Currently, there are no guidelines on what types of animal condition indices to include in such a comprehensive profile. This is largely due to a lack of performance evaluations of suites of indices correlating condition with population parameters, similar to the approach Dinkines et al. (1991) used to identify indices sensitive to differences in habitat quality. A more comprehensive study conducted by Bergeron and Jodoin

(1989) incorporated a suite of diet quality, morphometric, histologic, and physiological indicators, to detect density-related changes in animal condition in fluctuating populations of *Microtus pennsylvanicus*. Brown et al. (1995) conducted the most extensive comparisons of nutritional condition indices in deer under controlled feeding conditions where energy and protein levels in the diet were varied.

We examined the sensitivity of multiple condition indices to detect density-related changes in condition of white-tailed deer. Diet quality, morphometric, parasitic, histologic, and physiologic parameters were monitored in association with a decline in density of an over-populated white-tailed deer herd in Oklahoma (USA). Comparisons were made with a reference population where density was below carrying capacity of the habitat.

MATERIALS AND METHODS

Study area

We intensively monitored alterations in animal condition and health prior to (September 1988–September 1990) and immediately following (March 1991–March 1992) a decline in density of a severely overpopulated deer herd in Sequoyah State Park (SSP) located in northeastern Oklahoma (35°5′ to 36°0′N, 95°1′ to 95°2′W). The park is a 1,140-ha peninsula bounded by Fort Gibson Reservoir which constitutes 86% of its boundary. These geographic characteristics, which limit animal dispersal, in combination with no hunting since 1955 have resulted in severe overpopulation. Annual drive censuses in April indicated that deer densities were 80 and 72 deer/km^2 in 1989 and 1990 (designated the high-density study herd) and 39 and 41 deer/km^2 in 1991 and 1992 (designated the reduced-density study herd), respectively. For comparison, a reference deer herd well below carrying capacity (6 deer/km^2; spotlight census) was identified in northcentral Oklahoma (36°2′ to 36°4′N, 97°9′ to 97°11′W) and was sampled intensively during 1991 and 1992. This reference herd was selected because the deer population in northeastern Oklahoma has been above maximum sustainable density for many years (Shaw and Kocan, 1980).

Both deer herds occupy habitat on the western edge of the oak (*Quercus* spp.)-hickory (*Carya* spp.) forest, which is comprised mainly of upland forest, bottom hardwood forest, and eastern red cedar (*Juniperus virginiana*) savannas (Soper et al., 1993). Approximately 16% of SSP has been developed for recreational activities with turf-grass as the dominant vegetation type. Prominent browse lines and severe hedging of winged elm (*Ulmus alata*), green briar (*Smilax bona-nox*), and eastern red cedar throughout SSP suggested range quality was suboptimal. Mean temperatures for June to August in 1989, 1990, and 1991 were 25.2, 27.1, and 26.8 C, respectively; total rainfall levels for the period were 5.59, 1.61, and 3.65 cm, respectively.

Animal collection

Deer were collected from SSP in March and September of each year by live capture (March 1989–March 1992) and selective harvest (September 1988–March 1992). Deer from the reference herd were collected by selective harvest only. Live capture was accomplished using drop-nets over areas prebaited with corn, during early morning and late evening; prebaiting was limited to <5 days. Harvesting consisted of shooting adult does in the head or neck with a high-powered rifle over spotlights. Whole blood (3 ml EDTA-K tube) and serum samples (10 ml serum separation tube) were collected via heart puncture (harvested deer) or venipuncture (captured deer) and samples placed on ice. Hematological analysis was performed within 48 hr, and serum was separated by centrifugation within 6 hr of collection and was stored in aliquots at −80 C.

Evaluation of condition

Chest girth, hindfoot length, and age (tooth replacement and wear; Severinghaus, 1949) were recorded for all deer. An index of tick infestation was measured by enumerating ticks within a 2.54 cm circular template placed over the anus, eyes, and ears. Harvested deer were weighed (nearest 0.5 kg), and all major organs removed, trimmed of fat and connective tissue, and weighed (nearest 0.01 g) prior to recording eviscerated carcass mass; organ mass was expressed as a percentage of eviscerated carcass mass. Fat reserves were assessed using heart fat scores (HFS; Kistner, 1980), kidney fat index (KFI; Riney, 1955), and femur marrow fat content (FMF; Neiland, 1970). The abomasum was removed for determining the abomasal parasite count (APC; Eve and Kellogg, 1977). Other species of parasites encountered during gross necropsies were recorded as present or absent.

Tissue samples from lung, heart (base), liver, kidney, adrenal, pancreas, spleen, thymus, subscapular lymph node, bone marrow, and gas-

trocnemius muscle were preserved in a 10% neutral-buffered formalin for histological examination. Tissues were embedded in paraffin, sectioned at 5 to 6 μm thick, mounted on a glass slide, and stained with hematoxylin and eosin. Microscopic lesions were evaluated by a single pathologist without knowledge of treatment groups (i.e., high-density, reduced-density, reference herd). Lesions were graded as absent (0), minimal (1), mild (2), moderate (3), and severe (4), depending on type, size, and multiplicity; selected tissues from all harvested deer were examined histologically.

Hematology was performed using standard manual laboratory techniques (Sams et al., 1993), except in March 1992 when samples were analyzed on a Serono System 9000 Automated Cell Counter (Serono-Abaker Diagnostics, Allentown, Pennsylvania, USA) which was calibrated with our manual techniques above. Serum samples from March 1989–September 1990 were analyzed on an Olympus AU5000 chemistry analyzer (Olympus Clinical Instrument Div., New York City, New York, USA) at SmithKline Beecham Laboratory (Dallas, Texas, USA); samples collected in September 1988 and March 1991–March 1992 were analyzed on an Abbott EPX chemistry analyzer (Abbott Laboratories, Abbott Park, Illinois, USA) at The Family Medical Laboratory (Enid, Oklahoma, USA). Blood samples graded higher than slightly hemolytic or lipemic were omitted from analysis.

Index of diet quality

Dietary crude protein was indirectly monitored using a fecal nitrogen index (FN; Leslie and Starkey, 1985). Fecal pellets were recovered from the rectum of collected deer (March, September) and from the ground during seasonal field collections and analyzed for nitrogen using the Kjeldahl method (Jenks et al., 1989). Freshly defecated fecal pellets from 30 groups were collected from random locations throughout SSP in June, September, November, and December. Pellet groups were composited by season into 10 representative samples prior to analysis (Jenks et al., 1989).

Statistical analysis

Levene's test of homogeneity (Snedecor and Cochran, 1980) was used to identify heteroscadasitic variables, which were adjusted using log, square, and square-root transformation procedures (Sokal and Rohlf, 1981) prior to further analysis. Differences among herds (high-density, reduced-density, reference) for morphometric (including mass, and metric data) and physiologic indices were tested by 1-way analysis of variance for unequal sample sizes (PROC GLM; SAS Inst., 1982) for each capture method, season, gender, and age (adult or fawn) category. Separation among means was achieved using least squared means.

Data on parasite abundance (ticks, APC) were rank transformed to normalize their distribution prior to 1-way analysis of variance to test for differences among herds within each season (Conover and Iman, 1981). A log likelihood approximation (SAS Inst., 1982) was used to test for differences in the prevalence of histologic lesions and parasitic infections among herds. When significant, a Bonferroni Z statistic (Neu et al., 1974) was used to separate differences in mean prevalence.

RESULTS

Morphometric characteristics

The age structure of deer harvested from SSP (54% of individuals >3-yr-old) was considerably ($P < 0.05$) older than the reference herd (10% of individuals >3-yr-old). Deer harvested from SSP were morphologically under-developed; body mass, eviscerated carcass mass, chest girth, and hindfoot length measures were lower ($P > 0.05$) among high- and reduced-density herds compared to the reference herd in March and September (Table 1). Body mass of females harvested from high- and reduced-density herds averaged 18–26% less than reference does. Differences in body size between high- and reduced-density herds were limited to greater eviscerated carcass mass (14%; $P = 0.024$) and chest girth (6%; $P = 0.042$) for adult females harvested from the high-density herd in September, which was unexpected.

Relative masses of heart, kidney, liver, and thymus gland of harvested adult females differed ($P < 0.05$) among herds in March; organs averaged 14 to 33% less in mass from the high-density compared to the reference herd (Table 1). Thymus gland was the only organ that differed in mass between the reduced-density and reference herds, being 58% heavier ($P < 0.05$) in reference females in March. Relative heart, liver, and kidney masses increased ($P < 0.05$) among does harvested from the reduced-density compared to the

TABLE 1. Differences ($P < 0.05$) in carcass characteristics of adult (>1-yr-old) female white-tailed deer harvested from a high-density (80–72 deer/km^2), reduced-density (41–39 deer/km^2), and reference herd.

Character (unit)	High-density			Reduced-density			Reference			ANOVA (*P*-value)
	n	Mean	SE[a]	*n*	Mean	SE	*n*	Mean	SE	
March										
Body mass (kg)	18	41.8[b]	1.2	19	42.0[b]	1.2	6	51.4[c]	2.4	0.001
Eviscerated carcass mass (kg)	9	31.1[b]	0.9	19	30.3[b]	0.9	6	38.5[c]	1.8	<0.001
Chest girth (mm)	8	789[b]	12.7	19	808[b]	8.5	6	863[c]	17.3	0.003
Hindfoot length (mm)	14	406[b]	9.6	19	419[b]	3.3	6	445[c]	6.9	0.009
Kidney fat index (%)[e]	18	52.9[b]	7.2	19	22.4[c]	4.2	6	23.0[bc]	7.2	0.036
Relative mass (%)[f]										
Adrenal glands (paired)	9	0.014[b]	0.001	19	0.017[b]	0.001	6	0.010[c]	0.001	0.002
Kidney (paired)	9	0.26[b]	0.02	19	0.33[c]	0.01	6	0.33[c]	0.03	0.005
Liver	9	1.66[b]	0.07	19	2.33[c]	0.07	6	2.29[c]	0.12	<0.001
Heart[e]	9	0.98[b]	0.03	19	1.08[c]	0.02	6	1.14[c]	0.07	0.016
Thymus	9	0.024[b]	0.004	19	0.015[b]	0.003	6	0.036[c]	0.005	0.007
September										
Body mass (kg)	30	41.6[b]	1.2	9	38.3[b]	2.1	4	51.6[c]	2.3	0.005
Eviscerated carcass mass (kg)	20	30.0[b]	1.0	9	25.9[c]	1.2	4	37.3[d]	1.6	<0.001
Chest girth (mm)	20	754[b]	13.4	9	707[c]	15.3	4	832[d]	17.4	0.003
Hindfoot length (mm)	19	406[b]	4.2	9	409[b]	6.3	4	453[c]	12.2	<0.001
Femur marrow fat (%)	30	37.0[b]	2.0	9	24.1[c]	2.1	4	36.7[b]	5.9	0.008
Relative mass (%)[f]										
Adrenal glands (paired)	10	0.014[b]	0.001	9	0.015[b]	0.001	4	0.007[c]	0.002	0.008
Heart[e]	10	0.99[b]	0.03	9	1.14[c]	0.04	4	1.11[bc]	0.06	0.012

[a] SE = standard error.

[b–d] Values in the same row followed by different letters are significantly different ($P < 0.05$).

[c] Analysis performed on log transformed data.

[f] [parameter mass (g)/eviscerated carcass mass (g)] × 100.

TABLE 2. Histopathologic lesions observed in selected tissues of white-tailed deer from high-density (80–72 deer/km^2), reduced-density (41–39 deer km^2), and reference herds.

Lesion	High-density			Reduced-density			Reference			
	Number cases	% Frequency	Grade[a]	Number cases	% Frequency	Grade	Number cases	% Frequency	Grade	*P*-value
Kidney		(27)[b]			(37)			(19)		
Nephritis	6	22.2 [c]	2.7	20	54.1	1.6	8	42.1	1.4	0.033
Mineralization	1	3.7	1.0	11	29.7[+]	1.9	3	15.8	2.0	0.016
Adrenal		(27)			(37)			(19)		
Adrenalitis	4	14.8	2.3	8	21.6	1.8	1	5.3	2.0	0.231
Liver		(27)			(37)			(19)		
Periportal hepatitis	12	44.4	1.1	18	48.7	1.6	5	26.3	1.4	0.252
Multifocal hepatitis	6	22.2	1.2	4	10.8	1.8	1	5.3	2.0	0.207
Granulomatous hepatitis	1	3.7	1.0	7	18.9	2.4	8	42.1[+]	2.5	0.004
Lung		(26)			(37)			(19)		
Lymphoid aggregates	19	73.1	1.8	26	70.3	1.9	8	42.1	1.8	0.069
Parasitic granuloma	12	46.2	2.5	23	62.2[+]	3.0	0	0	0	<0.001
Interstitial pneumonia	4	15.4	1.5	3	8.1	1.3	1	5.3	2.0	0.485
Edema	2	7.7	2.5	0	0	0	1	5.3	1.0	0.150

[a] Mean grade of severity (1–4) of lesions for observed cases.
[b] Sample size in parenthesis.
[c] Lesion frequency was higher (+) or lower (−) than expected using a Bonferroni Z statistic.

high-density herd in March. The only difference in visceral organ development between high- and reduced-density herds in September was observed in relative heart mass ($P = 0.004$), which increased with a decline in density. Relative adrenal gland mass of does from either the high- or reduced-density herd was consistently 29 to 53% heavier ($P < 0.05$) than those from the reference herd in both seasons; mass between high- and reduced-density was not significantly different ($P > 0.05$). Relative masses of subscapular lymph node, popliteal lymph nodes, spleen, and pancreas did not differ ($P > 0.10$) among herds.

Levels of KFI in March were 58% lower ($P < 0.05$) in adult females harvested from the reduced-density herd compared to high-density animals; KFI of reference animals was intermediate (Table 1). Levels of FMF in does harvested from the reduced-density herd were 34% lower than both high-density and reference herds in September.

Histologic evaluation

Histologic examination of heart, pancreas, spleen, thymus, subscapular lymph node, bone marrow, and gastrocnemius muscle tissues did not reveal any remarkable lesions. Although cases of thymic involution and absence of bone marrow fat were observed, these were also reflected grossly by relative thymus mass and FMF. In contrast, eleven distinct histologic lesions were observed in kidney, adrenal, liver, and lung tissues (Table 2).

Prevalence of renal lesions (nephritis, mineralization) varied ($P < 0.05$) among herds. Specifically, prevalence of nephritis (46%) and mineralization (80%) was lower in deer harvested from the high-density herd compared to those from the reduced-density and reference herds. For deer harvested from the reduced-density herd, prevalence of nephritis did not differ but prevalence of mineralization was 39% higher than in the reference herd. Nephritis was characterized by multifocal, interstitial infiltrations of plasma cells and

lymphocytes located in the cortical or the medulla/cortical interface regions. Mineralization (multifocal and interstitial) was observed in the medullary region. Adrenalitis (multifocal lymphocytic infiltration in the medullary and/or medullary/cortical interface) was observed in 13 of 83 deer examined, with no difference in prevalence among herds ($P = 0.231$).

Hepatic lesions included multifocal and/or portal lymphocytic hepatitis and granulomatous hepatitis, which were characterized by the presence of lymphocyte, macrophage, and neutrophil aggregates and occasional giant cells. Granulomatous hepatitis was more prevalent ($P < 0.05$) in the reference herd (42%) than the high- (4%) or reduced-density (19%) herd. Portal hepatitis was observed in 42% and multifocal hepatitis in 13% of all animals examined, but prevalence did not differ ($P > 0.05$) among herds.

A high frequency (45/63 deer) of severe (2.5–3.0 grade) parasitic granulomas was observed in lung tissue of deer from the high- and reduced-density herds. Parasitic granulomas were not observed histologically in deer harvested from the reference herd. Severe parasitic granulomas were characterized by multiple large granulomas containing eosinophilic granular necrotic debris surrounded by epithelioid cells and macrophages. Eggs and larvae comparable with *Parelaphostrongylus* sp. were typically present in these granulomas. Perivascular and peribronchial lymphoid aggregates in the lung were very common (53 of 82 deer examined) among herds but did not differ ($P = 0.069$) in prevalence among herds. Other lung-associated lesions (interstitial pneumonia, edema) occurred at low frequencies (<10% of all deer examined) and did not differ ($P > 0.05$) among herds.

In general, parasitic infections were more prevalent or severe in deer from high- and reduced-density herds compared to reference animals (Fig. 1). Abomasal parasite counts and tick numbers were at least 3-fold greater among deer from high- and reduced-densities ($P < 0.05$) compared to the reference herd in March and September. Abomasal parasite counts declined with a reduction in density in September, but not March. The proportion of deer infected with nasal bots (*Cephenemyia phobifer*) and *Gongylonema pulchrum* also was higher ($P < 0.05$) in the high- and reduced-density herds than the reference herd in both seasons. Indices of tick abundance were 1.5 and 2.9 times greater ($P < 0.05$) at reduced-density than high-density in March and September, respectively. Nasal bot infections also were more prevalent ($P < 0.05$) at reduced-density than high-density in September, but not in March. Prevalence of *G. pulchrum* infections at reduced-density were 53 and 70% lower ($P < 0.05$) than high-density in March and September, respectively.

Physiologic evaluation

Because physiologic indices of condition are known to be sensitive to season and method of collection, we analyzed differences among herds separately for harvested and captured deer within each season. Captured deer were further analyzed by age (fawns as <10-mo-old and adults as >1-yr-old) and gender (adults) groups to control some of the variability due to factors other than density. Of all the physiological indices measured in our study, indicators of protein nutritional status appeared consistent in their response to herd density, regardless of collection method, season, age, or gender categories.

Concentrations of albumin and globulins were consistently the most sensitive physiologic indices of herd density (Table 3). The albumin/globulin ratio was extremely responsive to differing densities ($P < 0.001$) for collection methods, and season, age class, and gender categories. Differences in response to herd density also were exhibited in creatinine concentrations, which were higher ($P < 0.05$) among deer collected (harvested adult females in March and September, trapped adults in

March) at high-density compared to those from reduced-density or reference herds. Mean creatinine concentrations were 19 to 30% higher at high-density than reduced-density in March, regardless of collection method, age, or gender categories; the ratio of BUN/creatinine closely paralleled differences in creatinine. The only other consistent parameters observed among herds were serum transaminase (AST and ALT) and chloride levels. Concentrations of AST, ALT, and chloride did not differ ($P > 0.05$) among herds for harvested females but were consistently higher ($P < 0.05$) for captured deer from the reduced-density herd compared to those from the high-density herd. Chloride concentrations among all captured deer from the reduced-density herd were higher than the high-density herd during March but only adult males showed this trend in September.

Dietary nitrogen

Levels of fecal nitrogen varied ($P < 0.05$) between collection methods (rectal sample vs. fresh pellet groups), so data were analyzed separately. All deer collected from the high-density herd during March had fecal nitrogen levels averaging 27 to 39% below ($P < 0.05$) those from reduced-density or reference herds, regardless of collection method (Fig. 2). Levels of fecal nitrogen in harvested adult females from the reduced-density and reference herds did not differ ($P > 0.05$). Fecal nitrogen levels for deer captured in September and samples of defected feces removed from habitats in each season did not differ ($P > 0.05$) among herds.

DISCUSSION

It is important to state that sample sizes were often low for harvested deer and logistical constraints limited our ability to include replicated over-populated and reference herds in the study. However, despite these limitations, the study provided a useful comparison of many different condition parameters which were replicated across time. Herd density at SSP reached 80 deer/km^2, which was about 8-fold greater than the estimated carrying capacity for this oak-hickory forest habitat type (Torgerson and Porath, 1984). This was followed by a 2-fold reduction in density because of selective removal of does (harvest and trapping) and possibly other unknown factors. We continued to monitor the population for 2 yr following the reduction in density, but this would not be sufficient time for the habitat to fully recover from long-term over-browsing. However, we anticipated that a 2-fold reduction in density would effectively result in a 2-fold increase in the quantity of available forage (Hobbs and Swift, 1985).

Overall, the comprehensive condition profiles for deer from the high-density herd revealed evidence of density-dependent declines in condition resulting from nutrient limitations, increased parasitism, and presumed social stress. Physiological condition indicators suggested protein and energy availability were likely the predominant limiting factors at high-density. Morphometric and histologic (i.e., parasitic granuloma prevalence in lung tissue) characteristics of the high-density herd also were consistent with malnutrition and further suggested that this was a chronic condition. Seasonal monitoring of condition revealed that apparent nutrient deficiencies were most pronounced in March when levels of fecal nitrogen were lowest. Brown et al. (1995) demonstrated that both low protein and energy levels in the diet of deer are associated with reduced nitrogen levels in feces.

Gross morphometric parameters such as body mass and size differed among herds and provided the strongest evidence that nutrient deficiencies were chronic resulting in suppressed development (Severinghaus, 1955; McCullough, 1979). However, these indices provided little sensitivity to a 2-fold reduction in density from the high- to reduced-density herd over the 4 yr study. Delays in recovery of vegetation, induced chemical defense strategies of for-

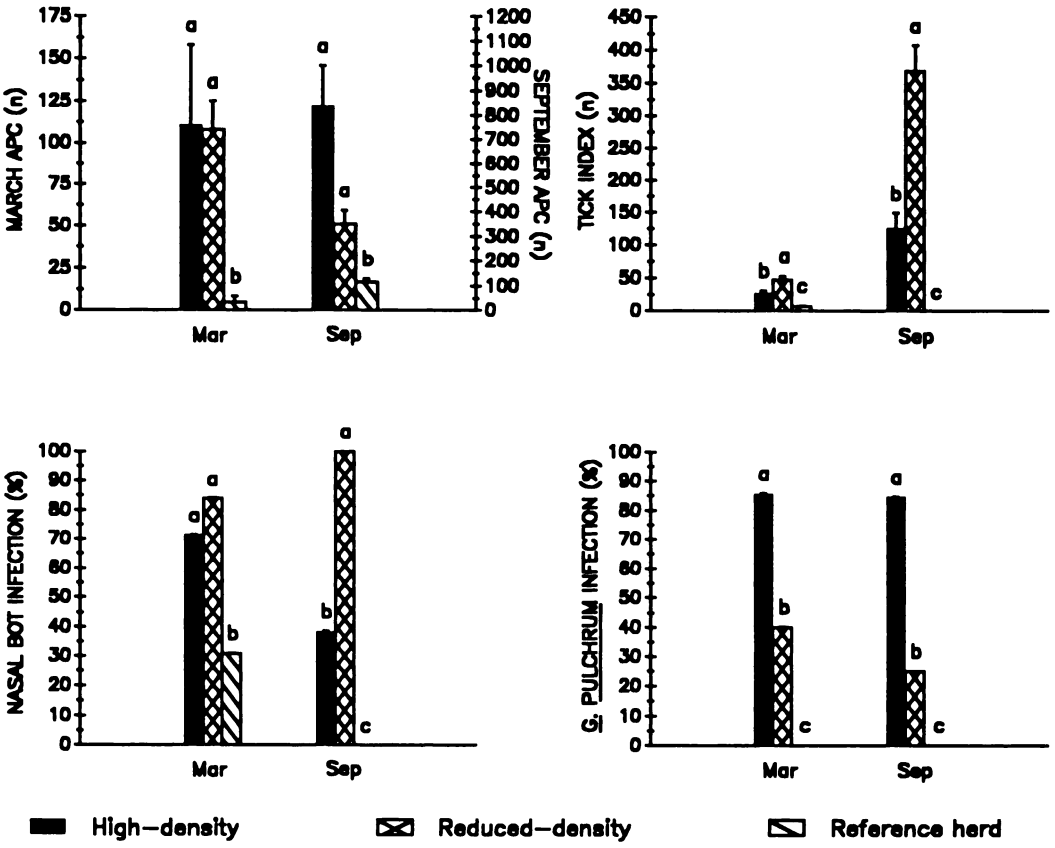

FIGURE 1. Severity (APC = abomasal parasite count, tick index) and prevalence (nasal bots, *G. pulchrum*) of parasitic infections in white-tailed deer collected from high-density (80–72 deer/km^2), reduced-density (41–39 deer/km^2), and reference herds. Values represent means (±SE); bars within season with no superscript in common indicate significantly different means ($P < 0.05$).

age, and suppressed early development have been offered as explanations for such lags in response of body mass to changing density (Fryxell et al., 1991). Compensatory growth in adult deer is poorly understood but likely is dependent on the duration and severity of malnutrition, the life stage which nutrients become deficient, and the degree of habitat rehabilitation (Kyriazakis and Emmans, 1992).

Observations that fat reserves (KFI, HFS, FMF) of deer from high-density herds did not differ from the reference population but did differ from the reduced-density herd were unexpected. Fat levels were similar to levels reported for other regional herds (Deliberto et al., 1989; Jenks, 1991; Soper et al., 1993). The lower fat levels of deer in the reduced-density herd coincided with lower eviscerated carcass mass and lower serum creatinine levels in September, suggesting that energy deficiencies persisted in the diet. This is certainly plausible given that the reduced-density herd remained well above carrying capacity. Additionally, fecundity may have increased in response to the reduction in density resulting in greater energetic demands on adult females. Brown et al. (1995) observed that KFI and carcass mass were lower in deer on low-energy diets, but they also noted that high protein levels in the diet reduced KFI.

Simple measurements of visceral organ mass provided some of the most consistent and sensitive responses during our study.

TABLE 3. Mean differences in blood constituents (± SE) of white-tailed deer collected from a high-density (80–72 deer/km^2), reduced-density (41–39 deer/km^2), and reference herd. Statistical analysis conducted using 1-way analysis of variance for each capture method, season, gender (adults), and age (adult or fawn) category. Blood constituents that did not differ significantly among herds are not shown.

	Harvested adult females			Trapped adult females		Trapped adult males		Trapped fawns	
Season Parameter (units)	High-density	Reduced-density	Reference	High-density	Reduced-density	High-density	Reduced-density	High-density	Reduced-density
March (n)	(11)	(19)	(6)	(40)	(8)	(7)	(11)	(17)	(10)
Blood urea nitrogen (mg/dL)	25.5	24.8	27.3	23.8	24.8	12.1	22.3°°	23.9	25.3
	(2.1)	(1.5)	(2.6)	(1.4)	(1.3)	(2.2)	(2.3)	(2.7)	(2.2)
Creatinine (mg/dL)	2.32[a]	1.79[b]	1.75[b]°°	2.41	1.91°°	2.37	1.90°°	2.08	1.75°
	(0.12)	(0.05)	(0.11)	(0.06)	(0.09)	(0.14)	(0.08)	(0.09)	(0.08)
Blood urea nitrogen/ creatinine ratio	11.4[b]	13.8[ab]	15.6[a]°	10.0	13.2°	5.0	12.0°°	11.7	14.7
	(1.2)	(0.8)	(1.1)	(0.6)	(1.0)	(0.7)	(1.4)	(1.3)	(1.4)
Total protein (g/dL)	6.09	6.48	5.97	7.08	7.60°	7.47	7.20	6.85	7.16
	(0.49)	(0.19)	(0.26)	(0.11)	(0.19)	(0.23)	(0.21)	(0.10)	(0.18)
Albumin (g/dL)	2.50[c]	2.93[b]	3.27[a]°°	2.84	3.91°°	2.89	3.35°°	2.88	3.42°°
	(0.06)	(0.09)	(0.13)	(0.04)	(0.17)	(0.06)	(0.09)	(0.05)	(0.11)
Globulin (g/dL)	4.05[a]	3.55[a]	2.70[b]°°	4.24	3.69°	4.59	3.81°°	3.98	3.74
	(0.14)	(0.19)	(0.19)	(0.09)	(0.26)	(0.20)	(0.16)	(0.08)	(0.13)
Albumin/globulin	0.62[c]	0.87[b]	1.25[a]°°	0.68	1.13°°	0.66	0.91°°	0.74	0.90°°
	(0.03)	(0.06)	(0.08)	(0.02)	(0.15)	(0.04)	(0.03)	(0.02)	(0.04)
Cholesterol (mg/dL)	39.5[b]	42.2[b]	51.0[a]°	48.4	52.8	56.3	46.1	48.9	46.5
	(1.7)	(1.9)	(5.1)	(1.8)	(3.4)	(4.5)	(3.2)	(1.8)	(5.3)
Total bilirubin (mg/dL)	0.64[a]	0.33[b]	0.37[b]°°	0.57	0.70	0.56	0.87	0.76	0.72
	(0.11)	(0.03)	(0.06)	(0.05)	(0.23)	(0.14)	(0.17)	(0.11)	(0.11)
Alkaline phosphatase (U/L)	65[a]	43[b]	104[a]°°	77	70	80	96	184	166
	(9.8)	(3.8)	(27.2)	(7.6)	(14.8)	(7.9)	(17.6)	(17.2)	(17.7)
Aspartate amino-transferase (U/L)	80	159	107	384	121	93	137°	147	163
	(9.2)	(42.5)	(25.2)	(130.6)	(8.1)	(6.2)	(14.3)	(15.3)	(19.4)
Alanine amino-transferase (U/L)	29.1	37.1	34.3	61.8	54.4	42.6	53.8°	46.6	69.5°°
	(1.5)	(2.0)	(4.8)	(13.8)	(5.2)	(3.5)	(2.4)	(2.3)	(2.8)
Calcium (mg/dL)	9.7[a]	8.3[b]	9.1[a]°°	9.4	8.9	9.7	9.3	10.1	9.2°°
	(0.2)	(0.2)	(0.2)	(0.1)	(0.2)	(0.2)	(0.2)	(0.2)	(0.2)
Phosphorus (mg/dL)	8.6[a]	7.1[b]	9.0[a]°	6.5	5.5	5.5	3.6°	7.0	5.9
	(0.5)	(0.3)	(0.7)	(0.3)	(0.4)	(0.5)	(0.5)°	(0.5)	(0.6)
Ca/P ratio	1.16	1.20	1.04	1.63	1.71	1.85	3.18°	1.59	1.72
	(0.06)	(0.04)	(0.07)	(0.10)	(0.20)	(0.14)	(0.46)	(0.14)	(0.20)
Chloride (mEq/L)	104	107	110	102	108°°	100	107°°	101	107°°
	(1.1)	(1.8)	(1.6)	(0.5)	(1.2)	(1.3)	(1.3)	(0.8)	(1.2)

TABLE 3. Continued.

Season / Parameter (units)	Harvested adult females			Trapped adult females		Trapped adult males		Trapped fawns	
	High-density	Reduced-density	Reference	High-density	Reduced-density	High-density	Reduced-density	High-density	Reduced-density
Red blood cells ($\times 10^6$/mm^3)	16.3	15.6	15.4	19.2	15.0°°	17.5	16.8	17.4	17.2
	(0.7)	(0.7)	(1.2)	(0.5)	(1.2)	(0.8)	(1.1)	(0.8)	(0.7)
Mean corpuscular volume (μm^3)	30.5	30.4	29.7	28.1	35.6°°	30.6	32.4	28.9	29.7
	(1.1)	(0.7)	(1.6)	(0.7)	(2.4)	(1.9)	(1.9)	(0.8)	(1.1)
Lymphocytes ($\times 10^3$/mm^3)	1.7	1.6	2.3	3.5	2.4	4.0	2.7°	4.1	3.8
	(0.5)	(0.2)	(0.8)	(0.2)	(0.3)	(0.5)	(0.4)	(0.6)	(0.5)
Eosinophils ($\times 10^3$/mm^3)	0.91[a]	0.46[a]	0.14[b]°°	0.37	0.55	0.33	0.75	0.43	0.64
	(0.26)	(0.06)	(0.04)	(0.05)	(0.17)	(0.07)	(0.14)	(0.12)	(0.13)
Monocytes (cells/mm^3)	5.8	8.3	18.1	5.0	24.8°	0	19.2	4.6	34.7°
	(4.7)	(5.3)	(11.9)	(3.0)	(9.9)	(0)	(8.9)	(4.6)	(14.9)
September (n)	(30)	(8)	(4)	(20)	(8)	(14)	(6)	(11)	(6)
Creatinine (mg/dL)	1.68[a]	1.48[b]	1.40[b]°	1.84	1.71	1.98	2.17	1.51	1.50
	(0.04)	(0.03)	(0.04)	(0.05)	(0.12)	(0.11)	(0.16)	(0.05)	(0.09)
Albumin (g/dL)	2.58[b]	2.84[ab]	3.08[a]°	2.59	3.30°°	2.69	3.38°°	2.73	3.42°°
	(0.07)	(0.07)	(0.14)	(0.07)	(0.07)	(0.04)	(0.13)	(0.05)	(0.13)
Globulin (g/dL)	3.78[a]	3.55[a]	2.85[b]°	4.42	4.17	4.34	3.90	3.31	2.97
	(0.11)	(0.18)	(0.15)	(0.13)	(0.23)	(0.17)	(0.19)	(0.14)	(0.14)
Albumin/globulin	0.71[b]	0.83[b]	1.10[a]°°	0.59	0.80°°	0.63	0.87°°	0.84	1.18°°
	(0.03)	(0.05)	(0.04)	(0.02)	(0.05)	(0.02)	(0.05)	(0.03)	(0.09)
Glucose (mg/dL)	114[b]	170[a]	134[ab]°	162	193	204	293°	186	193
	(9.4)	(23.0)	(26.0)	(9.9)	(29.7)	(14.1)	(38.5)	(14.0)	(13.5)
Total bilirubin (mg/dL)	0.32	0.35	0.65	0.23	0.42°°	0.41	0.55	0.79	1.20
	(0.04)	(0.04)	(0.21)	(0.03)	(0.05)	(0.08)	(0.06)	(0.16)	(0.29)
Alkaline phosphatase (U/L)	120[b]	131[b]	237[a]°	125	112	134	128	333	356
	(9.7)	(24.4)	(38.7)	(13.9)	(14.2)	(17.3)	(60.7)	(45.3)	(17.3)
Gamma glutamyl transpeptidase (U/L)	43.8[b]	37.5[b]	56.5[a]°	57.4	46.4	56.2	60.7	70.8	71.8
	(1.6)	(2.4)	(10.9)	(4.2)	(2.9)	(7.6)	(9.8)	(8.0)	(15.2)
Aspartate amino-transferase (U/L)	152	158	101	119	169°	121	163°°	124	177°
	(23.2)	(17.0)	(15.0)	(8.7)	(28.2)	(7.2)	(13.2)	(11.8)	(24.8)
Alanine amino-transferase (U/L)	54.7	57.5	48.3	43.0	65.1°°	47.7	66.2°°	46.5	87.5°°
	(3.8)	(4.8)	(6.1)	(2.9)	(3.9)	(2.9)	(6.7)	(3.3)	(4.4)
Lactic dehydrogenase (U/L)	498	691	601	544	812°	620	911	653	1254°
	(50)	(39)	(50)	(62)	(57)	(107)	(115)	(78)	(294)
Na/K ratio	16.8	15.3	16.5	30.0	32.5	28.8	29.5	30.5	24.9°
	(0.8)	(1.0)	(1.9)	(1.4)	(1.4)	(1.2)	(1.5)	(1.4)	(1.3)

TABLE 3. Continued.

Season Parameter (units)	Harvested adult females			Trapped adult females		Trapped adult males		Trapped fawns	
	High-density	Reduced-density	Reference	High-density	Reduced-density	High-density	Reduced-density	High-density	Reduced-density
Chloride (mEq/L)	104	106	107	101	106	99	107°°	105	107
	(0.8)	(0.8)	(0.3)	(2.1)	(1.5)	(1.4)	(1.6)	(1.9)	(1.1)
Hematocrit (%)	36.1	37.5	37.9	45.5	45.2	50.5	48.8	44.9	34.7°°
	(2.2)	(2.2)	(2.6)	(1.4)	(1.9)	(1.7)	(1.8)	(1.9)	(1.9)
Eosinophils ($\times 10^3$/mm^3)	0.29	0.52	0.43	0.47	1.07°	0.68	1.00	0.44	0.50
	(0.05)	(0.36)	(0.12)	(0.09)	(0.31)	(0.15)	(0.37)	(0.14)	(0.15)
Monocytes (cells/mm^3)	8.8	17.9	37.6	0	40.2°°	12.3	19.1	5.15	42.3
	(7.3)	(12.2)	(23.2)	(0)	(16.9)	(8.9)	(19.1)	(5.15)	(23.9)

[a–c] Means of harvested adult females followed by different letters are significantly different ($P < 0.05$).
° P-value < 0.05.
°° P-value < 0.01.

Both protein and energy deficiencies in the diet of white-tailed deer fawns during early growth have been observed to not only suppress body development but also organ growth (Verme and Ozoga, 1980a, b). Lower relative masses of kidney, liver, and heart in adult does from the high-density herd suggested that these easily obtained measures are extremely useful for assessing seasonal (most remarkable differences occurred in March) and density-related changes in condition. Histologic and serum enzyme profiles of the high-density herd were not consistent with organ dysfunction, suggesting that low masses were likely due to decreases in cell size and contents of protein and water (McNurlan et al., 1979; Church et al., 1971). Greater visceral organ masses following a decline in density (especially in March) could be similar to the regeneration of organ mass that has been reported in malnourished lambs following refeeding (Fattet et al., 1984; Kabbali et al., 1992a, b). These studies have shown that declines in fat deposition can occur during protein realimentation, which may explain the lower fat reserves observed in deer from the reduced-density herd. As with nearly all indices of condition, natural seasonal rhythms in organ mass must be considered when interpreting responses (Anderson et al., 1974; Dauphine, 1975; Ozoga and Verme, 1978). Differences in thymus gland size between the reference herd and the other herds can be attributed to the former's younger age structure.

Previous surveys of histopathologic lesions associated with over-populated deer herds are limited to brief accounts in Rausch (1950) and Seger et al. (1969). Our survey revealed that various minor hepatic and renal lesions are common in white-tailed deer from Oklahoma. Overall, histologic lesions were not informative of density-related changes in condition.

The association between nutritional status of a host and degree of parasitism has been well documented (Compton, 1987). The density-dependence of abomasal par-

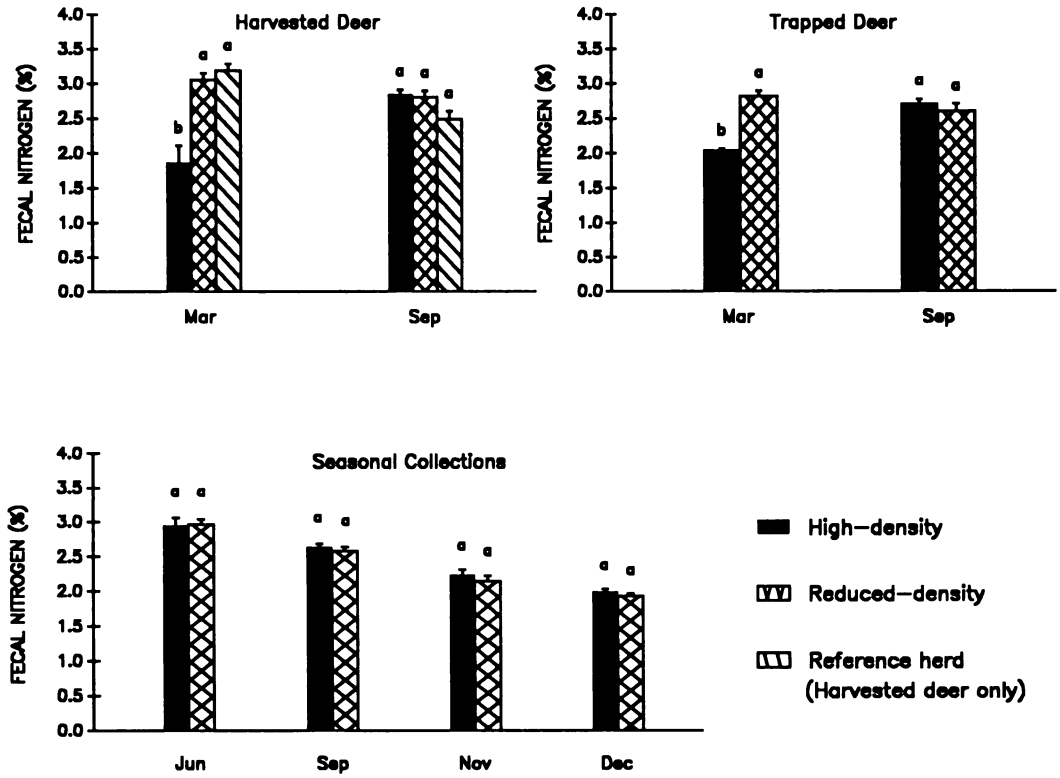

FIGURE 2. Levels of nitrogen in feces of sampled white-tailed deer (harvested and trapped) and seasonally collected pellet groups from high-density (80–72 deer/km^2), reduced-density (41–39 deer/km^2), and reference herds. Values represent means (±SE); bars within season with no superscript in common indicate significantly different means ($P < 0.05$).

asite counts in deer (especially in late summer to early fall) has been used to assess the relationship of populations to maximum sustainable density (Eve and Kellogg, 1977) or physical condition of individuals (Davidson et al., 1982). Although intensity of infections in Oklahoma are lower than in the southeastern states, the technique remains useful as indicated by the significant decline in September infections with a reduction in herd density. Infections of *G. pulchrum,* which has an indirect life-cycle, also demonstrated a density-dependent relationship.

Contrary to the above observations, nasal bot and tick infections showed a significant increase in the reduced-density herd. Hair et al. (1969) observed heavy nasal bot infections in over-populated herds in eastern Oklahoma and considered these to be a health risk to deer. Likewise, tick infections are frequently heavy when deer populations are dense (Patrick and Hair, 1977), leading to higher mortality rates of fawns in Oklahoma (Bolte et al., 1970). The decline in erythrocyte counts and increase in monocyte numbers in adult does coincided with elevated tick numbers, similar to the observations of Bolte et al. (1970). Heavy tick infections also can cause weight reductions, especially when animals are fed low quality diets (O'Kelly and Seifert, 1969), which might explain the observed reductions in carcass mass in the reduced-density herd. Higher infections in the reduced-density herd may be a reflection of fewer available hosts in an area where tick numbers in the environment (e.g., along game trails) has remained high. However, Patrick and Hair (1977) reported a significant reduction in tick infections of deer after a 20% decline

in deer density. June to August temperatures and moisture conditions are important factors influencing tick infection rates of deer in eastern Oklahoma (Patrick and Hair, 1977; Mount, 1981). Climatic conditions on our study areas were normal except during June to August 1990 (high-density herd) where normal temperatures (99% of normal) were accompanied by a mild drought (rainfall 35% of normal), which may have reduced tick survival and infection rates on deer (Mount, 1981).

Nitrogen components of serum (BUN, BUN/creatinine ratio, albumin, and total serum protein concentrations) have been reported to be sensitive measures of protein status in deer (LeResche et al., 1974; Kirkpatrick et al., 1975; Bahnak et al., 1979; Kopf et al., 1984; Brown et al., 1995). Of these indices, BUN and total protein were not useful as values for high-density deer were similar to reference animals and levels reported for other regional deer herds (Deliberto et al., 1989; Jenks, 1991). In comparison, the BUN/creatinine ratio and albumin levels appeared to be responsive to a reduction in density and levels for reference deer indicated that they were in better condition. These indices also showed similar trends between high-density and reduced-density herds regardless of capture method. Robbins et al. (1974) observed renal recycling of urea among protein-malnourished deer supplied with sufficient energy. Similar to our findings, Kie et al. (1983) observed low albumin concentrations, suggestive of severe protein malnutrition (LeResch et al., 1974; Hyvarinen et al., 1975), among deer in an enclosed high-density herd with low-protein intake. Warren et al. (1982) observed albumin levels to decline in fawns after 8 wk on a diet low in protein.

Other physiological indices were largely inconsistent in their response to changing herd conditions. An exception was an observed increase in AST and ALT concentrations with reductions in density. Serum enzymes are known to vary widely due to a variety of stress-associated factors (such as capture method), so many individuals routinely avoid these as indices of condition. Increases in serum transaminase levels in deer have been associated with low dietary energy (Seal et al., 1978) and growth (Tumbleson et al., 1970), possibly reflecting high levels of protein metabolism associated with compensatory growth. The lower indices of body fat reserves of deer in the reduced-density herd compared to the high-density herd suggests that energy defiencies existed in the diet.

Brown et al. (1995) noted that more detailed field examinations of the relationship between nutritional condition indices and population density are needed. The comprehensive suite of condition indices we examined indicated that many of these are sensitive to density changes. Simple, inexpensive measures of condition such as visceral organ mass, parasite indices, fecal nitrogen, and serum albumin concentration or BUN/creatinine ratio were the most sensitive to changes in density in this study. These observations support the conclusions of Brown et al. (1995) who noted that many of these same fecal, serum, and carcass indices provided useful diagnostic information for classifying the energy and protein nutritional status of deer in captivity. However, our study further indicated that the mass of selected visceral organs and measures of parasitic infection can provide useful information as well. Clearly, no single index of condition can be recommended but suites of indices as noted above and in Brown et al. (1995) can provide the necessary diagnostic information for descriminating nutritional status among white-tailed deer.

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