Nutritional condition and fertility of white-tailed deer (*Odocoileus virginianus*) from areas with contrasting histories of hunting

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Abstract: We evaluated the nutritional condition and pregnancy rates of 58 female white-tailed deer (*Odocoileus virginianus*) from five areas in Indiana, U.S.A., with differing herd densities and histories of hunting. We found significant differences among sites for five external measures of body size, six physiological indicators of nutritional restriction, and five internal postmortem measures of body size and fat reserves. Multivariate assessment of nutritional condition provided an appreciable increase in classification of deer to their site of origin relative to reliance on any single variable. In addition, postmortem variables and physiological indicators contributed significantly to our ability to correctly classify deer. Nearly all measures of nutrition or stress indicated that deer from sites hunted annually were in better nutritional condition than deer from sites hunted only once in the past several decades. Fertility rates differed significantly among the sites and varied inversely with density. Comparison with other studies within the central and northern hardwood regions suggests that weak density dependence in fertility rates occurs among adult does, although substantial reproduction still occurs when densities exceed 50 deer/km^2. Density effects become progressively stronger for first-year and yearling females, with reproduction in the former age group virtually ceasing when densities exceed 30 deer/km^2.

Résumé : Nous avons évalué la condition alimentaire et les taux de grossesse chez 58 femelles du Cerf de Virginie (*Odocoileus virginianus*) de cinq régions de l'Indiana, É.-U., où la densité des troupeaux et l'histoire des chasses sont très différentes. Nous avons constaté des différences significatives entre les sites quant à cinq mesures externes de la taille, six indicateurs physiologiques des restrictions alimentaires et cinq mesures internes postmortem de la taille et des réserves de graisses. L'analyse multidimensionnelle de la condition alimentaire s'est avérée un outil précieux de classification des cerfs en fonction de leur lieu d'origine, supérieur à toute autre variable considérée seule. De plus, les variables postmortem et les indicateurs physiologiques ont contribué significativement à la justesse de notre classification des cerfs. Presque toutes les mesures de la nutrition ou du stress ont indiqué que les cerfs des régions où la chasse est annuelle étaient en meilleure condition alimentaire que les cerfs où la chasse n'a eu lieu qu'une seule fois au cours des dernières décennies. Les taux de fertilité différaient significativement d'un site à l'autre, variant en fonction inverse de la densité. La comparaison de ces résultats avec ceux d'autres études entreprises dans les forêts de bois francs du centre et du nord indiquent que les taux de fertilité des biches adultes sont peu reliés à la densité, bien qu'il y ait encore un taux de reproduction important aux densités de plus de 50 cerfs/km^2. Les effets de la densité deviennent de plus en plus marqués chez les femelles de 1 an et les femelles de l'année et le taux de reproduction devient pratiquement nul chez les femelles de 1 an aux densités supérieures à 30 cerfs/km^2.

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Introduction

Deer (*Odocoileus*) are integral components of natural and managed ecosystems throughout much of North America. As is the case with many other temperate-zone ungulates, they can have substantial effects on the composition, distribution, and biomass of native plants (Alverson et al. 1988; Tilghman 1989; Gill 1992; Putnam 1996; Anderson 1997; DeCalesta 1997; Healy 1997; Waller and Alverson 1997). Well-studied species such as white-tailed deer (*Odocoileus virginianus*) exhibit several characteristics required of a desirable ecological indicator of forest condition (Hanley 1996). Information on the nutritional condition, i.e., the state of body components that are controlled by nutrition and that influence future survival and reproduction (Saltz et al. 1995), of an indicator species can be an important adjunct to other data on population dynamics and habitat use (Franzmann 1985; Harder and Kirkpatrick 1994). One limitation of past assessments of nutritional condition has been the attempt to characterize this multifaceted phenomenon with a single or few index variables. Use of a multivariate

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approach to quantify nutritional condition is desirable and could increase the discriminatory power of resulting comparisons among individuals and populations (Franzmann 1985; DelGiudice et al. 1990).

Nutritional condition may have a strong impact on dynamics of ungulate populations because it influences ovulation and conception rates, neonatal mortality, age at first reproduction, and number of offspring per birth event (Verme and Ullrey 1984; Gaillard et al. 1992; Chan-McLeod et al. 1995; Ouellet et al. 1997). Hence, monitoring of nutritional condition provides one means of assessing changes in a herd's demographic vigor (Chan-McLeod et al. 1995). Regular monitoring of white-tailed deer is warranted in many areas because their ecological and economic importance has situated them at the center of considerable scientific and public controversy (Swihart and DeNicola 1997).

In many areas, especially parks, refuges, and suburban localities, deer densities have increased steadily in recent years (e.g., Jones and Witham 1995; Underwood and Porter 1997). Reasons for these increases in deer numbers are disputed, but are likely due at least in part to the adaptation of white-tailed deer to early and midsuccessional habitats (Smith 1991). Deer populations presumably benefited from the extirpation of large predators by humans and the clearing of land for agriculture, with its concomitant fragmentation of habitat and increased availability of food (Smith 1991; Swihart et al. 1995; McCabe and McCabe 1997; Sinclair 1997). However, natural predation alone does not typically appear capable of regulating populations of most ungulates (Skogland 1991). Regulation refers to the process whereby a density-dependent factor stabilizes a population, whereas limitation refers to alteration of birth or death rates that changes abundance (Caughley and Sinclair 1994). Nor does food availability in and of itself appear capable of regulating populations of herbivorous mammals (Boutin 1990). Recent evidence indicates that ungulate populations in the absence of predation are unlikely to reach a stable equilibrium with their food resource (Sæther 1997). Moreover, populations of irruptive, unhunted deer can fluctuate without any apparent reduction in amplitude (McCullough 1997). Although largely incapable of regulation when operating alone, food and predation may interact to regulate populations of some mammalian herbivores (Krebs et al. 1995; Korpimäki and Krebs 1996), including ungulates (Sinclair and Arcese 1995).

Traditionally, wildlife managers have argued that hunting serves as a substitute for regulation by natural predators and prevents irruptions (reviewed by McCullough 1997). Hunting as a form of predation inarguably serves to limit herbivore populations, as does food availability (Ozoga and Verme 1982; McCullough 1984; Skogland 1985; Boutin 1990; Sinclair 1997). But critics of hunting contend that it has not conferred stability to many deer populations and that rigorous testing of hunting as a regulatory mechanism is lacking (Rutberg 1997).

Herein, we evaluate the ability of several morphological and physiological measures to discriminate among female white-tailed deer collected from populations representing a gradient of densities and vegetative quality in the midwestern United States. We also test whether variables collected from live deer provide a level of discrimination comparable with that observed when variables from postmortem evaluations are added. Finally, we examine whether fertility rates vary as a function of hunting history and population density.

Materials and methods

Study areas and deer history

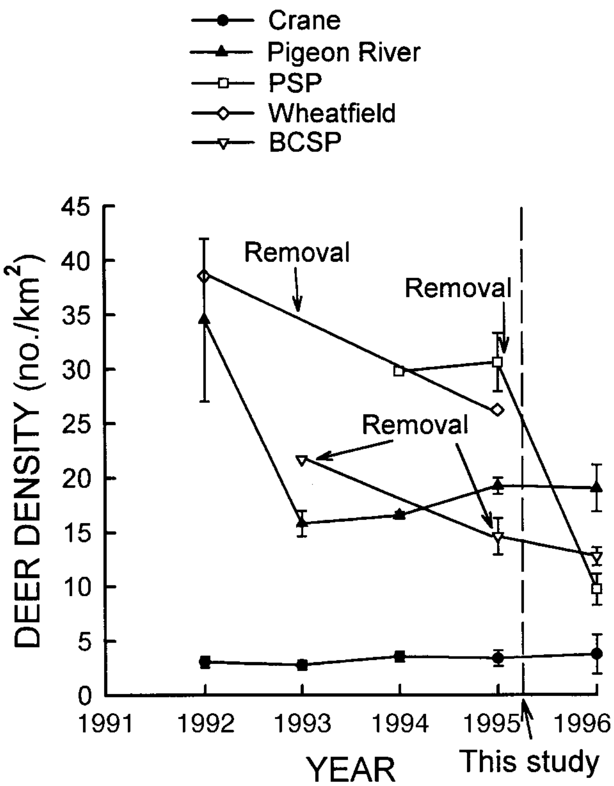
Following their extirpation from Indiana, U.S.A., at the beginning of the twentieth century, deer were reintroduced during the 1930s and received statewide protection from hunting until 1951 (Mumford and Whitaker 1982). Although hunting of deer in Indiana has been widespread since the 1950s, several areas remained unhunted until the 1990s. We collected data on physical and physiological characteristics of adult female white-tailed deer from five populations in Indiana during February and March 1996. The sites were chosen because they represented extremes in terms of their histories of deer hunting.

At two of the sites, Crane Naval Surface Warfare Center (hereafter called Crane) and Pigeon River Fish and Wildlife Area (hereafter called Pigeon River), deer have been hunted annually for several decades. Deer reportedly caused damage to vegetation on Crane before the advent of hunting in 1960 (reviewed by Kirkpatrick et al. 1976), but qualitative observations indicate that vegetation currently is in good condition. Crane is a 246.1-km^2 federal military facility in south-central Indiana. The site is dominated by second-growth hardwoods, which occupy about 70% of the area. Grass/forb areas are well distributed and available as mowed utility rights-of-way, roadsides, and openings surrounding storage magazines. Timber harvesting by group selection occurs throughout Crane. During the 4 days of gun hunting each year, 350–400 deer are harvested, divided approximately equally between males and females. During the years preceding our study, autumn prehunt density, which was estimated using the sum of pregun-hunt harvests and catch-effort data from gun hunts subjected to iteratively reweighted least squares (Bishir and Lancia 1996; Lancia et al. 1996), remained relatively stable at 2.8–3.8 deer/km^2 (Fig. 1).

Pigeon River is a 47-km^2 property in northeast Indiana operated by the Indiana Department of Natural Resources. There have been no reports of vegetative degradation caused by deer browsing at the site. Because Pigeon River is actively managed for production of wildlife, numerous food plantings and other habitat enhancement practices have been implemented there. During the 16-day buck-only hunting season in November, 61–145 antlered males were harvested each year from 1992 to 1995. No data were available on the abundance of does or fawns. To estimate the autumn prehunt density of the entire population, we estimated buck density using catch-effort data as described for Crane. We then multiplied buck density by 10 to estimate the size of the total prehunt population because antlered bucks commonly comprise only about 10% of populations in which they are the only age/sex class of deer subjected to legal harvest (McCullough 1984). Data on harvest by archery (both sexes) before the gun season were then added to the estimate of density. The resulting estimates revealed that the autumn prehunt density from 1993 to 1995 was fairly stable at 15.8–19.3 deer/km^2, although a density of 34.5 deer/km^2 was computed for 1992 (Fig. 1).

At the three remaining sites, deer had not been subjected to legal harvest for several decades. At Brown County State Park (BCSP) and Pokagon State Park (PSP), a long-standing state policy had prohibited hunting since the initiation of the parks in the 1920s, except for a 1-day archery hunt in Brown County in 1951 (Mitchell et al. 1997). BCSP is a 63.5-km^2 property in south-central Indiana. It is dominated by second-growth forest typical of

Fig. 1. Estimated density (±1 SE) of white-tailed deer at five sites in Indiana, U.S.A., from which deer were collected in February and March 1996 for assessment of nutritional condition and fertility. Solid symbols represent sites at which deer have been hunted on an annual basis for decades. Prior to our study, removal of deer was undertaken at the three sites with no history of hunting, represented by open symbols (PSP, Wheatfield, BCSP); the timing of these removals is indicated by arrows. Methods of density estimation precluded computation of a standard error for five of the 18 estimates (see text for methods used to estimate density).



the central hardwood region and shares with Crane a topography characteristic of the unglaciated southern portion of the state. Park personnel expressed concerns about the abundance of deer and their impacts on native vegetation in the 1980s, but no estimates of deer density were generated. Surveys of vegetation revealed considerable damage to herbaceous and woody species in the understory, including reductions in the growth of indicator species such as *Osmorhiza claytoni*, *Arisaema triphyllum*, and *Actacea pachypoda* relative to conspecifics on annually hunted control sites (Brown 1996; Webster 1997). After considerable debate, the park was opened for a 1-day hunt of deer in 1993 (Mitchell et al. 1997). An expanded 3-day hunt followed in 1995. Catch-effort data from the 1995 hunt yielded an estimated autumn prehunt density of 14.6 deer/km^2. We used the Leslie method (Krebs 1989) and the catchability computed from 1995 to estimate the prehunt density in 1993 as 21.7 deer/km^2 (Fig. 1).

PSP is a 4.9-km^2 property in northeast Indiana. The property is predominantly forest, with openings devoted to recreational activities (e.g., picnic areas, toboggan runs). The area may function as a forest fragment because it is isolated from other deer habitat by urban areas, a lake, and interstate highways. The understory has been heavily impacted by deer; significant reductions occurred in the three indicator species mentioned previously, and coverage by native plants has been reduced so severely that the site currently is dominated by the exotic invasive garlic mustard (*Alliaria petiolata*) (Webster 1997). A helicopter count in January 1995 yielded an estimate of 29.8 deer/km^2. Following a 3-day hunt in 1995, catch-effort data were used to estimate a prehunt autumn density of 30.6 deer/km^2 (Fig. 1).

The final study population was located near Wheatfield in northwest Indiana, at a coal-burning power plant operated by Northern Indiana Public Service Company. In addition to the power plant and associated structures, the site contains 6.5 km^2 inhabitated by deer. A 2.4-m chain-link fence was erected around the area in 1975, and deer inside the fence emigrated only rarely (DeNicola 1997). Hunting was prohibited on the area. Nearly the entire area was open grassland or savanna habitat on sandy soils; <5% of the site was forested (Swihart and DeNicola 1997). A survey of vegetation in forested areas during 1997 revealed a dearth of regeneration and evidence of heavy browsing by deer; none of the indicator species was present on the site, and virtually all woody species were heavily browsed, except for seedlings of *Prunus serotina* (S. Weeks, unpublished data). We captured and marked 109 deer with numbered ear tags during March–April 1993 as part of a study on contraception (DeNicola et al. 1997*a*, 1997*b*); density estimates derived from systematic sightings while driving road transects were 38.6 deer/km^2 in 1992 and 26.2 deer/km^2 in 1995 just before our removal (Fig. 1) (DeNicola 1997).

Hypotheses and predictions

We reasoned that if nutritional condition and fertility rates of deer vary inversely with density, then condition and fertility would vary from highest to lowest as follows: Crane > BCSP ≥ Pigeon River > Wheatfield ≥ PSP, based on 1995 estimates of density (Fig. 1). However, if differences in habitat condition are considered, the predicted rankings change slightly. Crane and Pigeon River have had no documented degradation of native habitat due to overbrowsing by deer for the past 25 years, and native food supplies at Pigeon River are supplemented with food plots. In contrast, vegetation at BCSP, PSP, and Wheatfield has exhibited severe overbrowsing by deer, with reductions in amount and species richness of herbaceous and woody understory vegetation (Brown 1996; Webster 1997; S. Weeks, unpublished data). We reasoned that if nutritional condition and fertility rates of deer varied as a function of habitat condition, then nutritional condition and fertility should vary from highest to lowest among the sites as follows: Crane = Pigeon River > BCSP = Wheatfield = PSP. Results intermediate between those predicted by the density and habitat hypotheses would be consistent with an interactive effect of deer density and habitat condition on nutritional condition.

Collection of data

Adult does were collected at each site with a single shot to the head from a .223-caliber rifle. An exception was PSP, where 6 of the 15 collected deer were immobilized remotely with a mixture of Telazol HCl and Xylazine HCl (DeNicola and Swihart 1997) and then euthanized. Twelve deer were collected at Crane and at BCSP, 9 at Pigeon River, and 10 at Wheatfield. All deer were collected between dusk and 03:30, and 79% were collected before midnight. Collections were conducted from 23 February to 15 March 1996.

We recorded three suites of measurements for each deer. External morphological measurements generally followed Feldhamer et al. (1985) and included body mass (kilograms), body length (centimetres), shoulder height (centimetres), chest girth (centimetres), ear length (millimetres), hind-foot length (centimetres), skull length (centimetres), and least interorbital breadth (millimetres). All appendages were measured on the right side of the body.

Physiological measures of condition were derived from blood and urine samples collected <30 min after euthanasia (<15 min in 81% of deer). Blood samples were collected in both polypropylene

Table 1. External condition measures for adult female white-tailed deer collected from five sites in Indiana during February and March 1996.

Variable	Study site				
	Crane	Pigeon River	BCSP	PSP	Wheatfield
Body mass (kg)	64.0*a* (1.3)	62.2*a* (2.6)	55.6*b* (1.4)	46.2*c* (1.3)	49.9*c* (1.7)
Body length (cm)	177.5*a* (1.9)	170.7*b* (2.5)	164.1*bc* (1.7)	159.3*c* (1.8)	168.1*b* (1.5)
Shoulder height (cm)	94.2*ab* (1.0)	93.1*bc* (0.6)	92.7*b* (1.2)	89.6*c* (1.0)	93.2*bc* (1.1)
Chest girth (cm)	92.6*a* (0.8)	94.8*a* (1.8)	88.4*b* (1.1)	83.5*c* (0.8)	87.8*b* (1.2)
Least interorbital breadth (mm)*	72.3*a* (2.2)	73.0*a* (0.7)	69.1*ab* (1.0)	67.5*ab* (1.4)	63.4*b* (3.1)

Note: Values are given as the mean, with the standard error in parentheses. For each variable, site means followed by the same letter do not differ significantly ($\alpha = 0.05$) as judged by a posteriori pairwise comparisons.

*Least interorbital breadth was not used when deriving PCs because damage to the skull was too severe to permit its measurement for 17 deer.

(10 mL) and EDTA (5 mL) tubes. After allowing blood in polypropylene tubes to coagulate on ice for 4–8 h, blood was centrifuged at 2500 rpm and serum removed with a pipette. Serum was then frozen for subsequent analysis of urea nitrogen (SUN), cortisol, and triiodothyronine (T_3) concentration. Blood in EDTA tubes was inverted 10 times to mix with heparin and kept refrigerated for <5 days before analysis of hemoglobin concentration and red blood cell count. Urine samples were stored frozen in polypropylene tubes for <5 days and then assayed for concentrations of urea nitrogen (N), sodium (Na), potassium (K), and creatinine. Results were expressed as ratios of urinary urea N : creatinine, Na:creatinine, and K:creatinine. All blood and urine assays were conducted by Wolff Laboratories, Minneapolis, Minn.

The suites of external and physiological measurements permit assessment of nutritional condition of live deer, and hence might be preferable under some circumstances. Internal postmortem measurements constitute a third suite of commonly used indexes of nutritional condition. We recorded eviscerated mass, adrenal mass, and gastrocnemius mass (right) as defined by Watkins et al. (1991). We also measured mass of decapsulated kidneys and perirenal fat, from which a kidney fat index (KFI) was computed as (mass of untrimmed perirenal fat/mass of kidneys) ×100 (Watkins et al. 1991). Fat depots around the heart, omentum, kidneys, rump, and brisket were combined with an assessment of body musculature and reported as a Kistner score (Kistner et al. 1980). We also determined femur marrow fat (Nieland 1970) and fat content of the gastrocnemius (Association of Official Analytical Chemists 1984; Folch et al. 1957).

For pregnant does, we recorded uterine mass, fetal mass, and number of fetuses. To assess the generality of any relationship between fertility and deer density at our study sites, we compared our data with data collected independently in other populations of the central and northern hardwood forest regions, including Illinois (Roseberry and Klimstra 1970; Nixon et al. 1991; Witham and Jones 1992), Indiana (White 1968; Hoekstra 1971; Stormer 1972; Kirkpatrick et al. 1976), Pennsylvania (Woolf and Harder 1979; Palmer et al. 1997), New York (Underwood and Porter 1997), and Ohio (Harder and Peterle 1974; Bell and Peterle 1975). We restricted our attention to the central and northern hardwood regions because they previously were shown to yield comparable fertility rates in deer (Sileo 1973).

Analysis of data

Initial comparisons among the five sites were conducted by subjecting each variable to either a nonparametric Kruskal–Wallis test or a one-way analysis of variance. Two-sample *t* tests were used with each physiological variable for deer from PSP to test if method of collection (rifle, immobilization/euthanasia) influenced blood and urine parameters (Seal et al. 1978*b*; DelGiudice et al. 1994). No significant differences were noted ($P \geq 0.22$ for all tests); thus, we pooled data from deer collected by these two methods.

We also examined pairwise correlations between variables to verify that significant collinearity existed, especially within suites of parameters. To reduce the redundancy contained in correlated variables within a suite, we conducted a separate principal components (PCA) analysis (SAS Institute Inc. 1994) on the subset of variables that had yielded a significant differentiation of sites in the univariate tests, except for least interorbital breadth, which was omitted because of small sample sizes. This procedure was repeated for each of the three suites of variables (external, physiological, postmortem). Only PCs with eigenvalues >1 were retained for subsequent analysis.

PCs derived from the three suites of variables were then used in a multivariate analysis of variance (MANOVA) and discriminant analysis (SAS Institute Inc. 1994) to determine the extent to which deer from the five sites could correctly be classified. Because public opposition, local ordinances, or other factors could preclude killing of deer in some localities (e.g., Hesselton 1991), we conducted an additional MANOVA and discriminant analysis after excluding the PC derived from postmortem variables. The cost of obtaining physiological profiles could preclude their use by some agencies; thus, we also conducted a MANOVA and discriminant analysis after excluding the PCs derived from physiological variables. We examined improvement in discriminatory ability using a test for additional information by Rencher (1995). All MANOVAs were conducted using age as a covariate.

Results

External measures of condition

The average age of females in the sample was 5 years (SE = 0.4 years), and no differences existed in age of deer collected among the sites (Kruskal–Wallis test, $T = 5.25$, $P = 0.26$). Univariate tests revealed significant differences among sites for five of the eight external variables (Table 1). Body mass was greatest for deer from Crane and Pigeon River, whereas mass was least for deer from PSP and Wheatfield. Chest girth also was greatest for deer from Crane and Pigeon River, whereas PSP deer exhibited the smallest mean girth. Measures of skeletal size (body length, shoulder height, and least interorbital breadth) generally indicated that deer from Crane and Pigeon River had the greatest skeletal dimensions, deer from PSP had the smallest skeletal dimensions, and deer from BCSP and Wheatfield were intermediate.

A PCA of body mass, body length, shoulder height, and chest girth (least interorbital breadth was omitted, see Table 1) yielded a dominant eigenvector that accounted for

Table 2. Physiological measures of condition for adult female white-tailed deer collected from five sites in Indiana during February and March 1996.

	Study site				
Variable	Crane	Pigeon River	BCSP	PSP	Wheatfield
SUN (mg/dL)	9.8*a* (0.9)	20.8*b* (1.8)	12.7*a* (1.2)	23.5*b* (1.7)	31.1*c* (2.2)
Serum cortisol (ng/mL)	1.9*a* (0.8)	9.0*ab* (4.1)	2.6*ab* (5.9)	10.3*b* (2.6)	5.0*ab* (0.8)
Serum T_3 (ng/dL)	218.1*a* (11.4)	223.0*a* (20.1)	190.0*a* (8.0)	104.3*b* (11.4)	100.9*b* (8.0)
Hemoglobin	18.2*ab* (0.4)	19.0*b* (0.5)	16.4*a* (0.7)	18.0*ab* (0.5)	17.5*ab* (0.3)
Urinary K:creatinine	0.41*a* (0.05)	0.33*a* (0.08)	0.38*a* (0.08)	0.82*b* (0.14)	0.81*b* (0.13)
Urinary urea N : creatinine	1.54*a* (0.21)	4.31*b* (0.33)	1.82*a* (0.32)	5.39*bc* (0.46)	6.37*c* (0.94)

Note: Values are given as the mean, with the standard error in parentheses. For each variable, site means followed by the same letter did not differ significantly (α = 0.05) as judged by a posteriori pairwise comparisons.

Table 3. Postmortem measures of condition for adult female white-tailed deer collected from five sites in Indiana during February and March 1996.

	Study site				
Variable	Crane	Pigeon River	BCSP	PSP	Wheatfield
Eviscerated mass (kg)	48.5*a* (1.1)	47.8*a* (2.0)	42.2*b* (1.0)	33.1*c* (0.7)	34.6*c* (1.0)
Gastrocnemius mass (g)	411*a* (11)	446*a* (20)	402*a* (11)	346*b* (10)	343*b* (13)
Gastrocnemius fat (%)	12.1*bc* (0.9)	16.4*a* (0.8)	14.1*b* (0.6)	10.2*cd* (0.6)	9.2*d* (0.7)
Femur fat (%)	91.7*a* (1.6)	90.2*ac* (1.9)	89.0*a* (3.5)	77.2*bc* (2.8)	66.6*b* (7.5)
KFI	373*a* (54)	290*ab* (60)	210*b* (20)	53*c* (7)	25*c* (6)
Kistner score	85*a* (2)	78*a* (4)	77*a* (2)	50*b* (2)	36*c* (2)

Note: Values are given as the mean, with the standard error in parentheses. For each variable, site means followed by the same letter did not differ significantly (α = 0.05) as judged by a posteriori pairwise comparisons.

74.4% of the total variation in the original variables. Coefficients of the eigenvector were comparable in size (0.52 for body mass, 0.52 for body length, 0.43 for shoulder height, 0.42 for chest girth), suggesting that the first PC derived from the external measures described a general body size variable.

Physiological measures of condition

Six of the eight variables of blood and urine profiles differed significantly among sites (Table 2). SUN and urinary urea N : creatinine displayed comparable patterns. Levels of these variables were lowest in deer from Crane and BCSP, significantly greater for deer from Pigeon River and PSP, and greatest for deer from Wheatfield. T_3 and urinary K:creatinine yielded identical patterns across sites, with greatest levels in deer from Crane, Pigeon River, and BCSP. For serum cortisol and hemoglobin, only a pair of sites differed significantly. Cortisol levels were significantly lower in deer from Crane than in deer from PSP. Hemoglobin levels were greater in deer from Pigeon River than in deer from BCSP.

A PCA of the blood and urine parameters in Table 2 yielded two eigenvectors with eigenvalues >1 (3.15 and 1.14). Together, these eigenvectors accounted for 71.5% of the total variation in the original variables. Coefficients of the dominant eigenvector (PC1) were 0.52 for SUN, 0.22 for cortisol, –0.44 for T_3, 0.02 for hemoglobin, 0.54 for urinary urea N : creatinine, and 0.45 for urinary K:creatinine. We interpret the first PC as a contrast of protein catabolism and dietary energy levels. Coefficients of the second PC were 0.09 for SUN, 0.22 for cortisol, 0.32 for T_3, 0.89 for hemoglobin, 0.17 for urinary urea N : creatinine, and –0.14 for urinary K:creatinine. We interpret the second PC as a measure of hemoglobin levels.

Postmortem measures of condition

Six of the seven postmortem variables resulted in significant differences among sites (Table 3). Eviscerated mass was greatest for deer from Crane and Pigeon River, intermediate for BCSP, and least for PSP and Wheatfield. Mean values for gastrocnemius mass and Kistner score were greatest for deer from Crane, Pigeon River, and BCSP. Mean values of KFI exhibited patterns comparable with eviscerated mass, except that KFI of deer from Pigeon River and BCSP did not differ. Femur fat was quite low in deer from Wheatfield.

A PCA of the variables in Table 3 yielded a dominant eigenvector that accounted for 66.2% of the total variation in the original variables. Coefficients of the eigenvector were comparable in size (0.45 for eviscerated mass, 0.40 for gastrocnemius mass, 0.35 for gastrocnemius fat, 0.36 for femur fat, 0.40 for KFI, 0.46 for Kistner score), suggesting that the first PC derived from the postmortem measures described a general measure of body size and fat reserves.

Discrimination among sites based on multivariate measures of condition

To quantify the degree of divergence in nutritional condition among the five populations using the PC scores, we used discriminant analysis. When all four of the PCs were used (one from external variables, two from physiological variables, one from postmortem variables), 83% of the deer were correctly classified into their herd of origin. By comparison, random assignment would correctly classify only 20% of the deer, on average. The MANOVA incorporating

Fig. 2. Fertility rates of adult does (≥ 2.5 years of age) from white-tailed deer populations in the central and northern hardwood regions of the United States with differing herd densities. In addition to this study, data are from earlier work in Indiana (White 1968; Hoekstra 1972; Stormer 1972; Kirkpatrick et al. 1976), Illinois (Roseberry and Klimstra 1970; Nixon et al. 1991; Witham and Jones 1992), Pennsylvania (Woolf and Harder 1979; Palmer et al. 1997), New York (Underwood and Porter 1997), and Ohio (Harder and Peterle 1974; Bell and Peterle 1975).

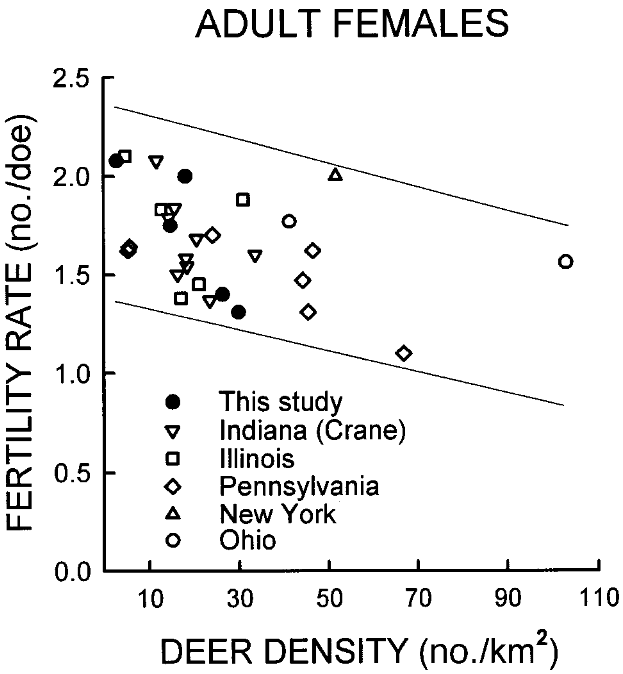
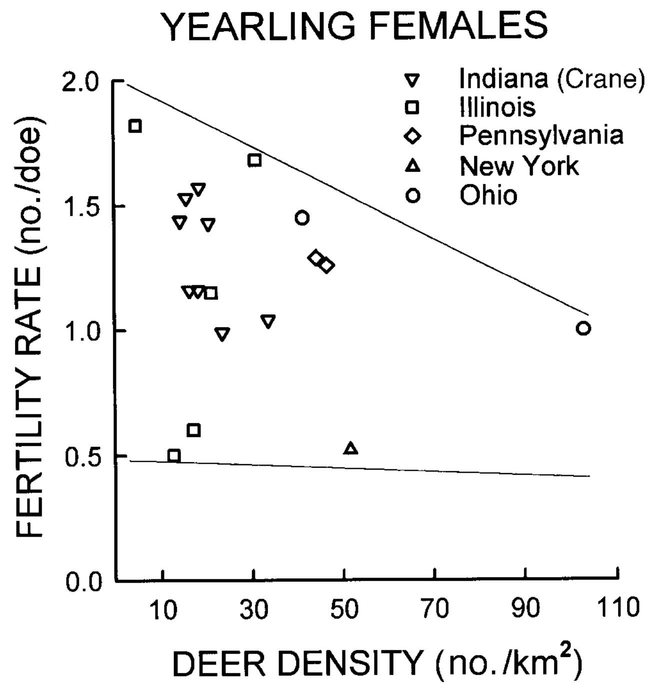


Fig. 3. Fertility rates of yearling does from white-tailed deer populations in the central and northern hardwood regions of the United States with differing herd densities (see Fig. 2 for literature sources).



all PCs exhibited significant differences among the five populations (Wilks' $\Lambda = 0.048$, $P = 0.0001$).

Elimination of the postmortem PC from the analysis reduced to 75% the deer correctly classified, but significant differences were still evident among the populations (Wilks' $\Lambda = 0.110$, $P = 0.0001$). Rencher's (1995) test for additional information compared Wilks' Λ for the full model (Λ_{full}) with Wilks' Λ for the model excluding the postmortem PC (Λ_{nopm}). For our study, inclusion of the postmortem PC contributed significantly to the separation of deer at the five sites ($P < 0.05$, $\Lambda^* = \Lambda_{full}/\Lambda_{nopm} = 0.435$; critical value of $\Lambda = 0.803$ with 1, 4, and 43 df).

Elimination of the PCs for physiological parameters reduced to 71% the deer correctly classified, although significant separation of the five herds was still noted (Wilks' $\Lambda = 0.102$, $P = 0.0001$). Application of Rencher's (1995) test indicated that inclusion of the physiological PCs contributed significantly to the separation of the herds ($P < 0.05$, $\Lambda^* = \Lambda_{full}/\Lambda_{noph} = 0.469$; critical value of $\Lambda = 0.700$ with 2, 4, and 44 df).

Fertility rates

Fertility rates differed significantly among sites (Kruskal–Wallis test, $T = 11.7$, $P = 0.02$). A posteriori comparison of z scores indicated that fertility rates (fetuses per doe) of deer from Crane (2.1 ± 0.2) and Pigeon River (2.0 ± 0.2) were significantly greater than fertility rates of deer from Wheatfield (1.4 ± 0.2) and PSP (1.3 ± 0.2). Deer from BCSP exhibited intermediate fertility rates (1.8 ± 0.2). Masses of individual fetuses also tended to vary among sites (Kruskal–Wallis test, $T = 8.4$, $P = 0.08$). Mean fetal masses arranged in ascending order were Wheatfield (361 g), BCSP (394 g), PSP (421 g), Crane (461 g), and Pigeon River (532 g).

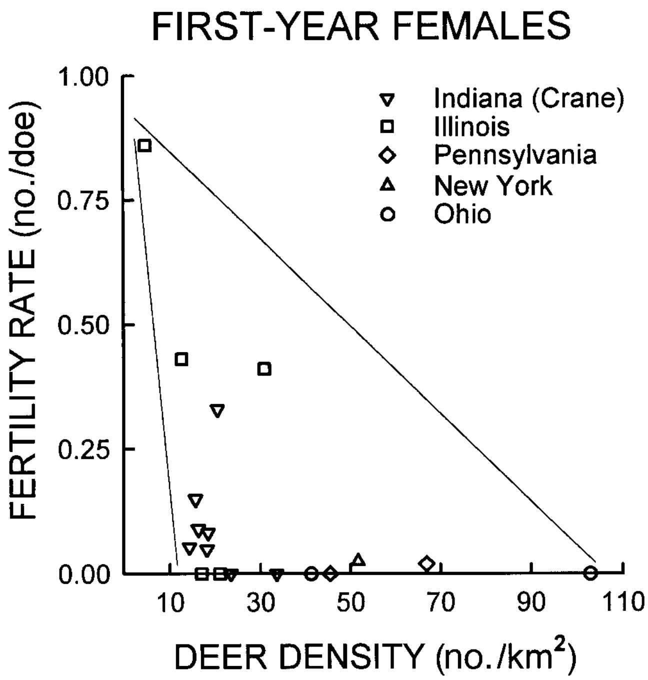
Fertility rates in our study were within the range of values reported for adult does in the central and northern hardwood regions (Fig. 2). Adult fertility rates exhibited only a weak inverse relationship with density. The minimum fertility rate represented a 48% decline relative to the maximum value reported for adults. Fertility rates of yearlings were considerably more variable than for adults, but exhibited a similarly weak inverse relationship with herd density (Fig. 3). The minimum fertility rate represented a 72% decline relative to the maximum value reported for yearlings. Fertility rates of fawns exhibited the strongest negative relationship with density, with reproduction virtually ceasing at densities >35 deer/km^2 (Fig. 4).

Discussion

Comparison of herds

Deer from the areas subjected to annual hunting (Crane and Pigeon River) were larger than deer from sites with little or no history of hunting, as determined by body mass, chest girth, and least interorbital breadth (Table 1). Differences in habitat condition appear to be responsible for this pattern, since the density of deer at Pigeon River was comparable to the density of deer at BCSP and four- to five-fold greater than the density of deer at Crane (Fig. 1). Vegetative degradation has been documented at BCSP, PSP, and Wheatfield,

Fig. 4. Fertility rates of first-year does from white-tailed deer populations in the central and northern hardwood regions of the United States with differing herd densities (see Fig. 2 for literature sources).



but no degradation has been evident at either Crane or Pigeon River since the advent of hunting (Brown 1996; Webster 1997; S. Weeks and G.R. Parker, personal communication).

In contrast to external morphological measures, which presumably reflect cumulative effects of nutrition and stress (Saltz et al. 1995) acting over long periods during somatic growth, parameters measured from blood and urine reflect short-term as well as longer term responses to nutrition and stress and hence are more labile indicators of nutritional restriction (Harder and Kirkpatrick 1994). Interpretational difficulties can arise if a blood or urine parameter is viewed in isolation, however, because relationships with nutritional condition often are not monotonic (Harder and Kirkpatrick 1994; DelGiudice 1995; DelGiudice et al. 1995). For example, levels of serum urea N and urinary urea N : creatinine when viewed alone suggest that deer from Crane and BCSP were in the early stages of undernutrition, whereas deer from the other three sites had suffered prolonged undernutrition (Table 2) (DelGiudice and Seal 1988). However, high levels of these variables can be either a result of catabolism of muscle tissue by deer that have depleted their fat reserves or a result of high dietary protein intake (Warren et al. 1982; Torbit et al. 1985; DelGiudice et al. 1990, 1994). Thus, their interpretation should be coupled with general information about range conditions, including extent of artificial feeding (DelGiudice 1995), and with other indicators of nutritional restriction. Potassium is an intracellular cation, and excessive excretion of K has been linked to prolonged stress in laboratory animals and implicated in the sharp decline of an island population of sika deer (*Cervus nippon*) in Maryland (Robbins 1983 and references therein). Muscle catabolism during starvation also can result in elevated levels of urinary K (DelGiudice 1995). Urinary K:creatinine was elevated for Wheatfield and PSP (Table 2), consistent with stress and prolonged undernutrition leading to muscle catabolism. In contrast, urinary K:creatinine was low for deer from Pigeon River (Table 2), which is not consistent with prolonged undernutrition or stress. In fact, T_3, which is indicative of dietary energy levels (Seal et al. 1978*a*), was quite high for deer from Pigeon River but much lower for deer from Wheatfield and PSP. Collectively, the results of SUN, T_3, and urinary urea N : creatinine and K:creatinine suggest that deer from Pigeon River were on a higher nutritional plane than deer at the other sites. This interpretation is consistent with the availability of supplemental plots of winter food at Pigeon River and the observation that soybeans were still available to deer during March. We cannot determine the cause underlying the apparent high plane of nutrition for deer at BCSP as indicated by blood and urine parameters (Table 2). Adult does at BCSP were stunted relative to deer at Crane and Pigeon River (Table 1), which suggests a chronic state of undernutrition. Although the decline in population density achieved by removals in 1993 and 1995 could have been important (Fig. 1), we also suspect that the short-term condition of deer at BCSP was improved substantially by a bumper mast crop during fall 1995 in southern Indiana (S. Weeks, personal observation).

Postmortem measures of size (eviscerated mass, gastrocnemius mass) yielded results consistent with external measures and indicated that deer from Crane and Pigeon River were larger than deer from Wheatfield and PSP, with deer from BCSP intermediate in size (Table 3). Both the KFI and the Kistner score suggested that deer from the sites hunted annually were in excellent nutritional condition relative to deer from sites hunted only once. Marrow fat is the last reserve mobilized by deer (Harris 1945), and hence, fat content of femur marrow has been used as an index of severe undernutrition (Mech and DelGiudice 1985). Based on these measures of fat deposition, deer from Wheatfield were seriously undernourished (Table 3).

Utility of a multivariate approach

By using linear combinations of variables, we were able to correctly classify 83% of the deer into their appropriate herd. An even larger percentage (100%) could have been attained by using all variables, but we chose to categorize variables into suites to address the utility of variables collected via different methods and at different costs. The classification accuracy of the multivariate method exceeded the accuracy obtained using single variables, which ranged from 30 to 62%. In addition to improving discriminatory power, a multivariate approach has the advantage of incorporating into an analysis indexes of condition, stress, or nutrition that affect individuals on vastly different time scales. Although our findings suggest that multivariate approaches will be useful in comparative studies, the validation and limits of resolution of such an approach must await rigorous testing under conditions where energy and protein intake are manipulated experimentally over varying periods. Classification of herds differing only slightly in nutritional condition undoubtedly would require larger sample sizes than those used in our study.

Declines in classification accuracy were relatively small when postmortem (8% decline) and physiological (12% decline) PCs, respectively, were omitted from the multivariate analysis. Nonetheless, these declines were highly significant, suggesting that discrimination in nutritional condition among deer can best be done using information obtained from external morphological, physiological (blood and urine), and internal postmortem samples. If constraints preclude collection of all measures, we suggest the use of body mass, chest girth, eviscerated mass, KFI, Kistner score, SUN, T_3, and urinary K:creatinine and urea N : creatinine.

Role of population density and habitat condition

Two of our sites, Pigeon River and BCSP, offered contrasting levels of habitat condition at comparable densities, and this contrast formed the basis for the differing predictions made by the density hypothesis and the habitat condition hypothesis. Our tests of the predictions produced mixed results. External measures of body size that describe massiveness conformed more closely to the predictions of the habitat condition hypothesis, as did the physiological measures T_3 and urinary K:creatinine. But in no instance did our results match exactly the predictions of either hypothesis. Intuitively, increasing density of deer should reduce a herd's resource base, leading to declines in habitat condition. Recovery of habitat often will lag behind reductions in density, and long-term effects of previous undernutrition may still be detectable (Table 1). Thus, the functional dependence of habitat condition on density, coupled with inherent time lags in habitat recovery, makes it difficult to avoid confounding of these variables. However, Tilghman (1989) demonstrated experimentally that deer densities >15 deer/km^2 retard regeneration of deciduous hardwood species and alter tree species composition in northwestern Pennsylvania. She also noted a corresponding increase in overwinter mortality of deer occurring at densities >15 deer/km^2. Mortality was due to starvation and exposure, indicating a clear association among deer density, resource availability, and nutritional condition. In our study, deer in Indiana suffered from relatively severe undernutrition and reduced fertility at densities >25 deer/km^2.

Fertility rates of does from sites hunted annually were significantly greater than for sites hunted only once before the study, and density dependence in fertility rates of adult does in Indiana seems likely (Fig. 2) over a density range of 5–30 deer/km^2. In fact, the density dependence may be stronger than indicated in Fig. 2 because the catch-per-unit-effort estimates derived for Crane, BCSP, and Pigeon River could underestimate the actual density at these sites by 20% or more (see Lancia et al. 1996). In a matriarchal society, younger and subordinate females should be more sensitive to the effects of density than older, dominant females. The data in Figs. 2–4 bear this out; adult females maintained substantial, albeit slightly reduced, fertility rates even at densities >50 deer/km^2. Yearling females also continued to bear offspring at high densities, although their response was much more variable and the magnitude of decline appeared to be greater. But first-year females exhibited strong density dependence in fertility rate, with an almost complete cessation of reproduction at densities >30 deer/km^2.

One possible criticism of our study is its inability to demonstrate that long-term hunting of sites can contribute to reduced deer density. However, the initial year of hunting at PSP, BCSP, and Wheatfield produced reductions in deer density of 68, 33, and 32%, respectively (Fig. 1). Moreover, a second year of removal at BCSP was associated with a further reduction in density, a result that has been repeated at several state parks in Indiana that had not been hunted previously (Webster 1997; C.R. Webster, unpublished data). Finally, density estimates collected at Crane from 1960 to 1971 demonstrate an overall decline of 58% in association with the advent of hunting on an annual basis in 1960 (Hoekstra 1971; Stormer 1972).

In conclusion, multivariate assessment of nutritional condition permitted us to accurately differentiate among adult does collected from sites hunted annually and from sites where deer had been subjected to a single removal over the past several decades. These differences corresponded broadly to differences in density of deer at the sites. Fertility rates also were density dependent, and the strength of density dependence was age specific in the central and northern hardwoods region of the United States.

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