Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female white-tailed deer in Minnesota

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Weights, hematology, and serum profiles of white-tailed does in the central Superior National Forest of northeastern Minnesota were examined year-around to determine seasonal patterns of nutritional condition and metabolism. Deer were initially captured by Clover trap or rocket net. Between 15 February 1989 and 23 January 1990, we recaptured 12 adult (>1.5 years) female deer 1–9 times each (a total of 59 recaptures) using a radio-controlled capture collar. Monthly weights of deer exhibited a cyclic seasonal pattern. Mean weight declined 22% from February to an annual minimum during May, then steadily increased 45% to a maximum in October. Seasonal patterns were most evident for hemoglobin concentration, red blood cells, packed cell volume, serum total protein, urea nitrogen, creatinine, the urea N to creatinine ratio, triiodothyronine, cortisol, and potassium. Wide seasonal variations of these characteristics were indicative of shifts in the deer's metabolic physiology. Although seasonal metabolic shifts are partially attributable to an endogenous rhythm, the intensity of their expression was most likely affected by nutritional changes and concomitant alterations of body condition. Annual changes in seasonal trends of blood characteristics may be useful in investigating nutritional effects of specific environmental and demographic factors. We compare our findings with those reported for deer on ranges farther south.

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La masse, l'hématologie et les profils sériques de biches du Cerf à queue blanche dans le centre de la forêt Superior National Forest du nord-est du Minnesota ont été déterminés au cours de toute une année, dans le but d'établir les patterns saisonniers de la condition physique et du métabolisme. Les animaux ont d'abord été capturés au moyen de pièges Clover ou de filets lancés. Entre le 15 février 1989 et le 23 janvier 1990, nous avons recapturé 12 femelles adultes (>1,5 ans) 1–9 fois chacune (total de 59 recaptures) au moyen d'un collier de capture contrôlé par radio. Les masses mensuelles des biches suivaient un cycle saisonnier. La masse moyenne a diminué progressivement de 22% entre février et la valeur minimale en mai, puis a augmenté graduellement de 45% jusqu'à un maximum en octobre. Les effets saisonniers étaient apparents surtout dans l'hémoglobine, les érythrocytes, l'hématocrite, les protéines sériques totales, l'azote de l'urée, la créatinine, le rapport N de l'urée à créatinine, la triiodothyronine, le cortisol et le potassium. Les variations saisonnières importantes de ces caractéristiques reflétaient des changements dans la physiologie métabolique des animaux. Bien que les changements métaboliques saisonniers soient en partie attribuables à des rhythmes endogènes, l'importance de leur manifestation est plus susceptible d'être affectée par des modifications alimentaires et les modifications concommittantes de la condition physique. Les changements annuels des tendances saisonnières des caractéristiques du sang peuvent être de bons indicateurs des effets alimentaires de facteurs environnementaux et démographiques spécifiques. Nous comparons nos résultats à ceux d'études antérieures sur des cerfs de régions plus australes.

[Traduit par la rédaction]

Introduction

Increasing our knowledge of seasonal nutritional condition and metabolic patterns of free-ranging deer (*Odocoileus* spp.) is essential to expanding our understanding of their nutritional requirements, and indeed every aspect of their ecology (Leopold 1933, pp. 253, 302; Robbins 1983, p. 1). It has become increasingly clear that physiological, behavioral, and morphological adaptations enhance a deer's ability to survive the often harsh nutritional challenges presented by seasonal environmental perturbations (French et al. 1955; Ozoga 1968; Rongstad and Tester 1969; Silver et al. 1969; Seal et al. 1972; Moen 1976, 1978).

Survival and productivity of deer are dependent upon weight (Verme 1962, 1967; Moen and Severinghaus 1981), which is related to seasonal changes in available nutrition and metabolism (Silver et al. 1969; Moen 1978). Weight changes of deer are associated with changes in body fat, protein, and water levels (Jacobsen 1978; Torbit et al. 1985; DelGiudice et al. 1990*a*). The annual cycle of deer weights, specifically with respect to month of maximum and minimum weights, differs

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with geographical location, ecological conditions, and the sex and age of deer (Moen and Severinghaus 1981; Kie et al. 1983; Waid and Warren 1984; DeLiberto et al. 1989). There are no reports of year-around weights of deer in the northern part of their range.

Determination of hematologic characteristics and serum parameters that are sensitive to nutritional variation permits seasonal changes in metabolic physiology to be examined (Rosen and Bischoff 1952; Seal et al. 1981). Specific serum constituents reflect the intake of crude protein, energy, and electrolytes, as well as the degree of endogenous protein catabolism and fat exhaustion (Anderson et al. 1972; Seal et al. 1972; Kirkpatrick et al. 1975; DelGiudice et al. 1987). Such research has been conducted primarily with captive deer, in more or less controlled environments. These studies have helped to establish reference values and to elucidate the physiological response of deer to changes in their nutrition.

However, captive studies do not consider the influence of natural diets or natural activity and energy budgets of deer, nor the full impact of many environmental perturbations. Most of the variation in wildlife population trends is ascribable to the effects of environmental perturbations (Caughley 1970; Botkin et al. 1981; Goodman 1987), and nutrition is the link.

Sequential study of weights and blood profiles of free-ranging deer circumvents the limitations of captive studies and permits the in-depth examination of seasonal metabolic physiology essential to understanding the population−environment relationship. There is little information regarding year-around hematological characteristics of free-ranging deer (Anderson et al. 1970; Kie et al. 1983; DeLiberto et al. 1989), and to our knowledge, no year-around hematological data have been reported for white-tailed deer on northern ranges.

Only a few studies have included examination of seasonal weights and serum profiles; these involved white-tailed deer (*Odocoileus virginianus*) collected on ranges in Texas (White and Cook 1974; Kie et al. 1983; Waid and Warren 1984) and Oklahoma (DeLiberto et al. 1989) and mule deer (*Odocoileus hemionus*) in Colorado (Anderson et al. 1972). The findings of such studies are geographically specific. The difficulty of capturing white-tailed deer during snow-free seasons, and a variety of associated logistical constraints, have precluded such year-around studies of northern white-tailed deer (Seal et al. 1981).

We used a radio-controlled capture collar (Wildlink™ Recapture Collar) to periodically recapture free-ranging white-tailed deer with minimal stress (DelGiudice et al. 1990*b*; Mech et al. 1990). Such conditions are essential to the accuracy of such a nutritionally oriented study (Seal et al. 1981). Our objective was to examine seasonal patterns of the nutritional condition and metabolism of female white-tailed deer by monitoring weights and blood profiles year-around.

Materials and methods

Study area

The study area was a 2500-km^2 east-central portion of the Superior National Forest in northeastern Minnesota (48°N, 92°W) (Nelson and Mech 1981). Generally, the area is characterized by rolling topography and elevations of 400−700 m.

The study area consists of 76% upland and 24% lowland vegetation (Peek et al. 1976). Mixed coniferous−deciduous stands predominate on the uplands and include balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), and northern white cedar (*Thuja occidentalis*) (Nelson and Mech 1981). Beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), red-osier dogwood (*Cornus stolonifera*), and speckled alder (*Alnus rugosa*) are among the apparent browse species on uplands (Wetzel et al. 1975; DelGiudice et al. 1989*a*). Conifer swamps are associated with lowlands; black spruce (*Picea mariana*), tamarack (*Larix laricinia*), northern white cedar, bog birch (*Betula pumila*), and Labrador tea (*Ledum groenlandicum*) are abundant.

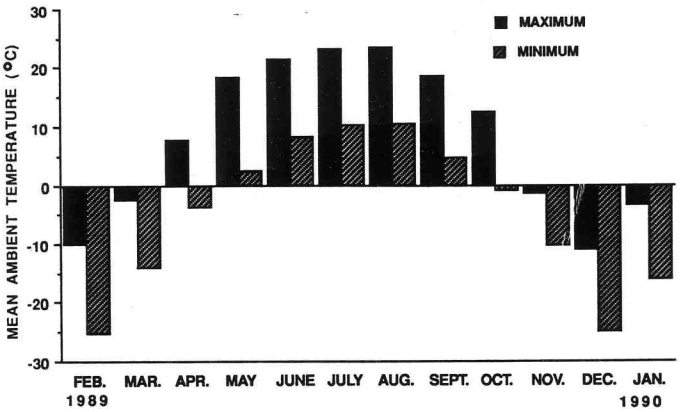

FIG. 1. Mean maximum and minimum monthly ambient temperatures for Isabella, Minnesota, February 1989 − January 1990. (Missing values for February and December 1989 were supplemented with data from Hibbing and Gunflint, Minnesota, respectively.)

During the study, mean maximum and minimum monthly temperatures ranged from −10.8 to 23.6°C and from −25.2 to 10.7°C, respectively (Fig. 1). Mean cumulative snowfall from mid-November to May is 150 cm (Nelson and Mech 1981). During the study, maximum monthly snow depth ranged from 3 to 78 cm during November and March, respectively (National Oceanic and Atmospheric Administration 1989, 1990). The winter severity index (WSI, Verme 1968) for the study area was 200 during winter 1988−1989 (Minnesota Department of Natural Resources, unpublished data).

Deer capture, recapture, and handling

Initially, we captured deer with Clover (1956) traps or by rocket net (Hawkins et al. 1968) and handled them as previously described (DelGiudice et al. 1990*b*; Mech et al. 1990), which included fitting each deer with a radio-controlled capture collar. Age of deer was estimated by cementum annuli of an extracted last incisor (Gilbert 1966). Between 15 February 1989 and 23 January 1990, we recaptured 12 adult (>1.5 years) female deer 1−9 times each (a total of 59 recaptures) using the capture collar. To minimize the potential for adverse effects on fawning, we did not recapture does during June. The presence of fawns or the occurrence of lactation in does during summer confirmed pregnancy of several does during spring; however, such follow-up evidence was not available for all does. The interval between recaptures of the same deer ranged from 14 to 57 days. Seventy-eight percent of these intervals were ≥21 days.

We located deer by radiotelemetry and triggered darts from 60−2000 m away. Deer were immobilized with either 213 mg phencyclidine HCl (PHEN) and 75 mg xylazine HCl (XYL) or 750 mg Telazol (375 mg teletamine HCl and 375 mg zolazopam HCl) (DelGiudice et al. 1990*b*; Mech et al. 1990). Five minutes of inactivity, monitored by an activity sensor (Kunkel et al. 1991) in the collar, indicated induction of anesthesia. Mean induction time was 13.0 ± 1.9 (SE) and 7.8 ± 0.9 min for PHEN−XYL and Telazol, respectively. Anesthesia was maintained with intramuscular injections of ketamine HCl (150 mg) or XYL (50 mg). During immobilization we collected blood into ethylenediamine tetraacetic acid vials and serum tubes by venipuncture of the jugular vein. Mean times between chemical induction and blood sampling were 36.4 ± 3.1 and 35.6 ± 2.6 min for PHEN−XYL and Telazol, respectively. Deer were weighed to the nearest 0.5 kg; rectal temperature was monitored, and used

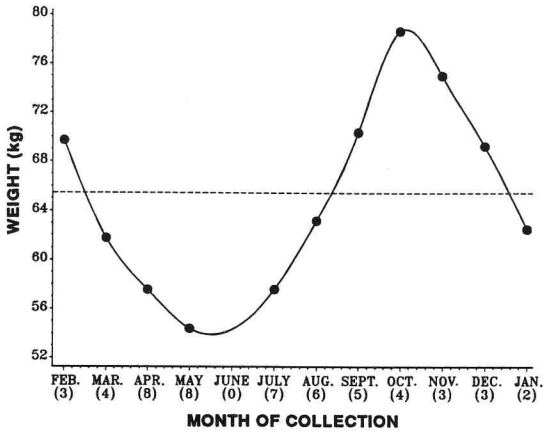

FIG. 2. Mean monthly weights of adult female white-tailed deer in the Superior National Forest, northeastern Minnesota, February 1989 – January 1990. Numbers in parentheses are sample sizes.

capture-collar darts were replaced with loaded darts. For deer injected with XYL, 15 mg of yohimbine HCl was administered intravenously before release (Mech et al. 1985). Deer also received a prophylactic intramuscular injection of a long-lasting penicillin preparation (1.5×10^6 units) (Dual-Pen™), Fermenta Animal Health Co., Kansas City, MO 63178, U.S.A.).

Blood analysis

Hematological analyses were conducted according to Seal et al. (1967) and DelGiudice et al. (1990*a*). Concentrations of serum total protein, urea nitrogen (N), creatinine, triglycerides, calcium, and inorganic phosphorous were determined on an Abbott VP bichromatic autoanalyzer using prescribed methods (Abbott Laboratories 1984). Sodium and potassium were measured by flame photometry. We determined total circulating thyroxine (T_4) and triiodothyronine (T_3) concentrations by solid-phase ^{125}I radioimmunoassay (Diagnostic Products Corp., Los Angeles, CA 90045, U.S.A.). Serum cortisol was also measured by radioimmunoassay (Cambridge Medical Technology Corp., Billerica, MA 01865, U.S.A.).

Data analysis

During this study, monthly data were collected from 12 deer. Due to various constraints it was not possible to recapture every deer in every month; thus, monthly sample sizes vary. Occasionally, two samples were collected from the same deer in the same month. To avoid the analytical problems that tend to arise from such incompletely repeated measurements, repeated measurements on each deer were replaced by their respective monthly means.

In analyzing the data, we have avoided the use of inferential statistics (i.e., tests and (or) confidence limits). Logistical problems associated with deer capture constrained us to limit sample sizes to levels that do not warrant analysis by inferential statistics. With small sample sizes, the power of the tests (and conversely the width of the associated confidence intervals) would invite type II errors. Furthermore, most of the appropriate tests depend on asymptotic properties and hence become increasingly unreliable as sample sizes decline from the recommended minimum of 25–30. Therefore, we confined our analyses to descriptive techniques for detecting and explaining patterns among the monthly measurements.

To examine the possibility that weight and individual blood parameters exhibited pronounced patterns of seasonal variation, we computed monthly means for each and plotted them over time. Since we did not have any *a priori* expectations of linearity in the seasonal relationships, we chose to fit a nonlinear path through the monthly data points for each parameter. Accordingly, monthly means were joined by fitting a cubic spline to the data (Wold 1974; Buse and Lim 1977; Smith 1979). In this procedure, data points were connected by a series of piecewise cubic polynomials so as to form the simplest continuous smoothed curve that will pass through every point in the sample. Frequently, such curves have inflection points with values that are larger or smaller than those observed in the data. This is analogous to the situation in which none or few observed data points actually lie on a least-squares regression line. Both the least-squares regression line and the cubic spline represent a "best guess" of the path of the underlying straight line or curve, respectively, but do not require that every point on the curve correspond to an observed data point. Once the splines were fit, a question of general interest was whether the observed pattern represents real seasonal variation or merely random "white noise" oscillations around a constant mean. Visual examination of this question is accomplished by overlaying the annual grand mean of the monthly parameter estimate on its corresponding spline. Sustained systematic departures from the grand mean were interpreted as evidence for nonrandom seasonal effects.

No attempts were made to draw statistical inferences from the relationships in our sample of 12 deer to the larger population. However, we do argue in the Discussion for a more general interpretation of our findings.

During the year, we recognized five seasons: late winter (1 February – 31 March), spring (1 April – 20 June), summer (21 June – 22 September, fall (23 September – 31 November), and early winter (1 December – 31 January).

Results

Age and weights

Mean age of deer sampled over the course of the study was 2.9 ± 0.3 (SE) years ($n = 53$). Mean monthly weight of these deer reflected a cyclic pattern (Fig. 2). Weight declined 22.0% from February to an annual minimum in May and steadily increased (44.6%) to a maximum value in October, followed by a progressive decrease through January.

Hematology

Mean red blood cell (RBC) count and packed cell volume (PCV) exhibited similar cyclic seasonal patterns characterized by markedly decreasing values from March to July and subsequent pronounced increases through October (Fig. 3). Mean hemoglobin (Hb) concentration varied similarly; however, the increasing trend in values did not occur until after August and generally persisted through December (Fig. 3). During October, RBC count and PCV were 35.0 and 19.2% greater than in July, respectively. Relative to July, Hb was elevated by 25.0 and 29.7% during October and December, respectively. Mean corpuscular hemoglobin (MCH) exhibited a seasonal rhythm, with primary peaks during spring and early winter (Fig. 3).

Plots of white blood cells (WBC), mean corpuscular volume (MCV), and mean corpuscular hemoglobin concentration (MCHC) did not exhibit pronounced seasonal patterns (Table 1).

Serum profiles

Monthly total protein concentrations increased progressively from April to October, then declined steadily through early winter (Fig. 4). During October, mean total protein concentrations were 21.3% higher than the minimum value in April. Conversely, serum urea N concentrations generally increased 131.8% from February to May, then declined 70.5–72.3% by October and November (Fig. 4). The monthly pattern of creatinine values reflected a nonrandom seasonal rhythm (Fig. 4). Mean concentrations decreased 41.3% by July, then increased 98.3% by October. The ratio of serum urea (urea N/0.466) to creatinine increased through May (51.4), then generally decreased 78.9% through October (10.9) (Fig. 4).

Serum T_3 values remained diminished during late winter,

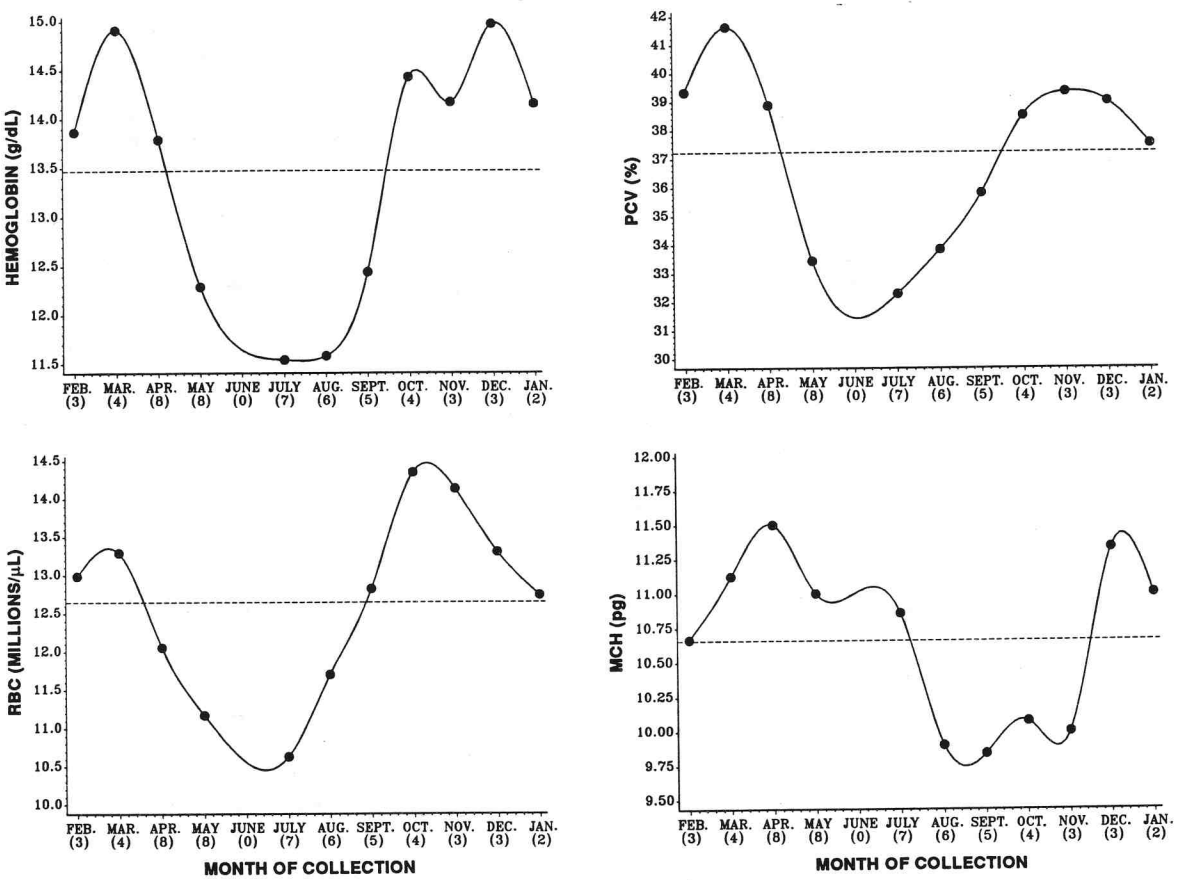

FIG. 3. Mean monthly values for hematological characteristics of adult female white-tailed deer in the Superior National Forest, northeastern Minnesota, February 1989 – January 1990. Numbers in parentheses are sample sizes.

but steadily increased 185.6% by September (Fig. 4). This was followed by a sharp decline (55.3%) by October, with values remaining diminished through early winter. Cortisol exhibited a bimodal pattern: concentrations increased sixfold from February to July, peaked again during September–October, then remained low through early winter (Fig. 4). Conversely, potassium decreased 51.4% from February to July, remained low through September, then increased 105.8% by December to values similar to those observed during February (Fig. 4). Seasonal patterns of concentrations of T_4, sodium, calcium, phosphorus, and triglycerides were obscured by random variation (Table 1).

TABLE 1. Blood characteristics that did not exhibit seasonal rhythms in adult (≥1.5 years) female white-tailed deer in the Superior National Forest, Minnesota, February 1989 – January 1990

	Mean	SE	Range
WBC ($10^3/\mu L$)	3.1	0.2	1.0–5.8
MCV (fL)	29.9	0.4	25.0–37.0
MCHC (g/dL)	35.8	0.2	29.0–40.0
Thyroxine (μg/dL)	12.1	0.4	7.0–19.5
Sodium (mequiv./L)	145	0.7	135–157
Calcium (mg/dL)	8.5	0.1	6.6–9.7
Phosphorus (mg/dL)	4.3	0.3	0.9–7.7
Triglycerides (mg/dL)	16.0	1.2	2.9–44.5

Discussion

Weight cycle

The seasonal weight variation of deer in north-central Minnesota exhibited a cyclic pattern similar to that predicted for white-tailed deer in central and northern New York (Moen and Severinghaus 1981). Adult females in New York that succumbed to winter undernutrition by February–March lost 30–37% of their fall weight (Severinghaus 1981), and estimated ratios of maximum fall weight to winter "weight of no return" (i.e., irreversible undernutrition) ranged from 1.4 (central Adirondacks) to 1.8 (central and Southern Tier regions of New York) for 2- to 3-year-old does (Moen and Severinghaus 1981). If we assume similar October weights during 1988 and 1989 for our deer (2.9 years old), the ratio of maximum weight (October) to minimum winter weight (March) was 1.3 and represented a weight loss of 21.5%. However, this ratio, calculated with the minimum monthly weight of early spring (May), was 1.4, and was associated with a 30.8% weight decline. These weight losses reflected the severe winter (WSI = 200) endured by our deer. A winter severity index ≥125 is considered detrimental to free-ranging deer in Minnesota (Verme 1968; P. D. Karns, Minnesota Department of Natural Resources, personal communication). Because only 1 of 9 deer captured during May was lactating (30 May), and assuming all other deer were pregnant, it is likely that the actual difference in doe weights between May and October exceeded 30.8%.

The weight loss tolerated by free-ranging deer during winter

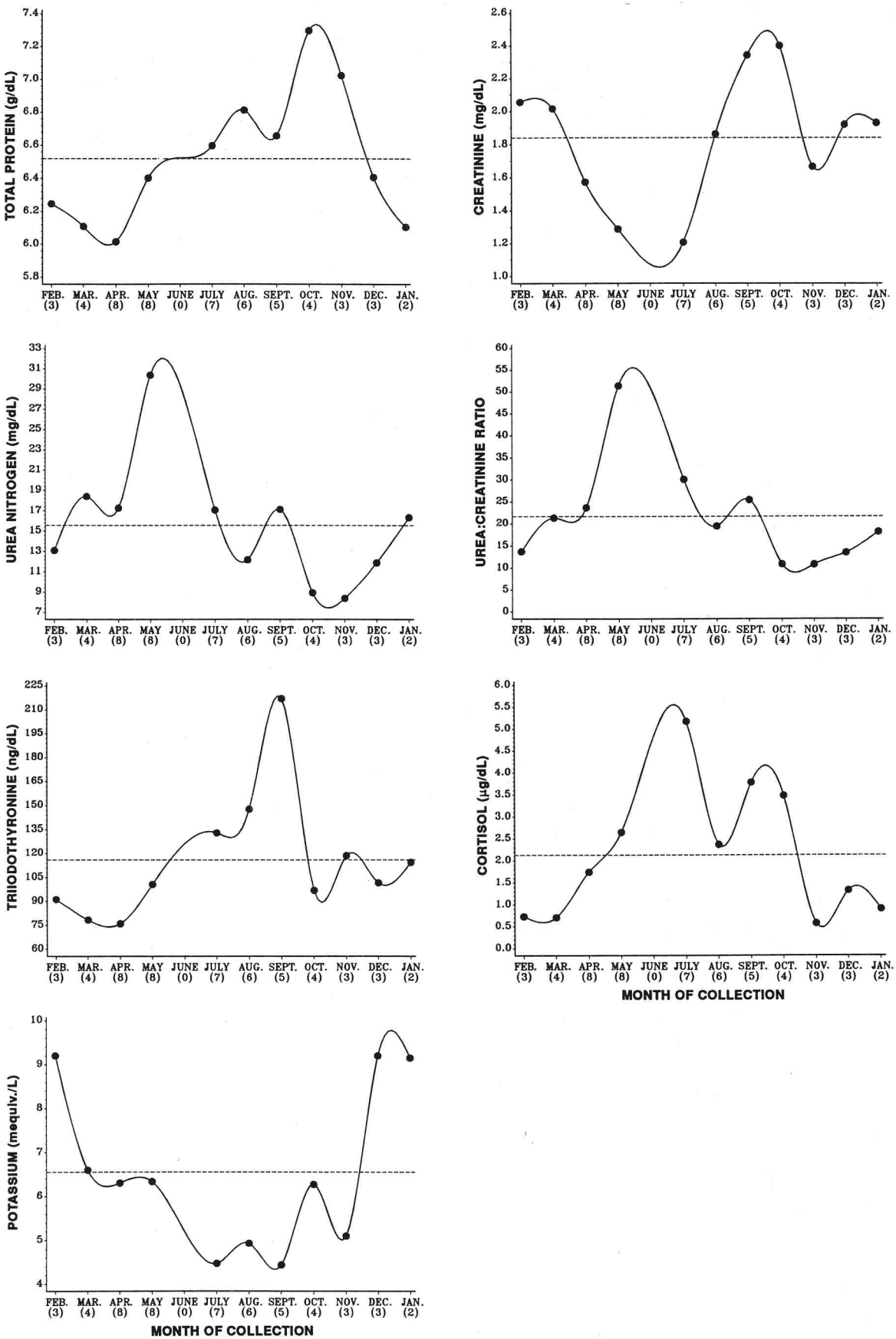

FIG. 4. Mean monthly values for serum characteristics of adult female white-tailed deer in the Superior National Forest, northeastern Minnesota, February 1989 – January 1990. Numbers in parentheses are sample sizes.

and early spring largely depends on their maximum weight during fall and the combined effects of winter severity and thermal cover (Davenport 1939; Moen and Severinghaus 1981; Severinghaus 1981). Generally, northern white-tailed deer can safely lose 30% of their fall weight; however, losses considerably greater have been observed (Davenport 1939; Severinghaus 1981). Maximum fall weight of our deer (78.6 ± 3.3 kg) was most comparable to that of deer in the central and Southern Tier regions of New York (67.5 ± 0.7 kg) (Severinghaus 1981). Using the ratio of maximum fall weight to weight of no return (1.8) of these New York deer (Moen and Severinghaus 1981), we estimated that our deer have a weight of no return of 43.6 kg, which represents a potential maximum weight loss of 44.5%.

DeLiberto et al. (1989) reported the absence of significant seasonal variation in eviscerated carcass weights of adult white-tailed does in south-central Oklahoma, apparently attributable to mild winters, limited snow cover, and "emergence of cool-season grasses and forbs ...." Weights of white-tailed does in central Texas, collected every 2–3 months, varied seasonally (Waid and Warren 1984). Mean weights were at a minimum during August, but were similar during the remainder of the year in that study. Kie et al. (1983) observed maximum and minimum weights during May and September, respectively, in adult deer in southern Texas.

Hematology

Hematological profiles of deer are affected by nutrition, and changes in certain characteristics may be used as indicators of nutritional status and general health (Seal et al. 1981; Bubenik and Brownlee 1987; DelGiudice et al. 1987). Hemoglobin concentration and PCV were most elevated during winter, specifically in March, and were associated with a mean weight that was 21.5% less than the peak mean weight during the following October. Elevation of Hb and PCV, as well as RBC counts, indicated a hemoconcentration that is directly attributable to the dehydration that accompanies nutritional deprivation and weight loss (Young and Scrimshaw 1971; Benjamin 1981, p. 73). Jacobsen (1978) reported parallel decreasing trends in relative plasma volume and weight of captive deer in New York from November–December to March–April as feed intake declined. Elevations of Hb, RBC, and PCV have been observed in captive undernourished white-tailed deer that lost a mean of 17.5–24.0% of their weight during winter (Seal et al. 1972; DelGiudice et al. 1987).

Anemias induced by undernutrition during winter may be concealed by the hemoconcentration that accompanies seasonal dehydration and decreased plasma volume. The larger MCVs (15.1%) during March–April than in the following fall, when deer were in peak condition, indicated a macrocytic anemia and enhanced erythropoetic activity in response to the anemia (Benjamin 1981, p. 128). From March to July, 22.6, 20.0, and 22.4% declines in Hb, RBC, and PCV, respectively, associated with decreased weights of deer that were similar to their yearly minimum weights (May), reflected the seasonal expansion of plasma volume that accompanies the increased feeding activity and intake of succulent vegetation during spring and early summer (Ozoga and Verme 1970; Jacobsen 1978).

The changes in hematological characteristics also coincided with late gestation and parturition. In 5 captive pregnant adult does, we noted declines in Hb, RBC counts, and PCV from early April (15.3 ± 0.3 g/dL, 12.2 ± 0.4 × $10^6/\mu$L, and 39.6 ± 0.4%) to mid-April (13.9 ± 0.4 g/dL, 11.1 ± 0.5 × $10^6/\mu$L, and 35.4 ± 1.0%), which remained stable at least until early May (G. D. DelGiudice, unpublished data). Slight declines in Hb, RBC counts, and PCV also occur during late gestation in domestic cattle and sheep (Ullrey et al. 1965; Benjamin 1981, pp. 102–103). Relative plasma volume reaches a peak in adult does by June and again in October (Jacobsen 1978). It was apparent from lower Hb, RBC counts, and MCHCs in our deer during summer than in fall that they were still anemic. Such an anemia tends to be related to nutritional deficiencies (Benjamin 1981, p. 130).

Subsequent increasing trends in monthly Hb, RBC counts, and PCV and decreasing MCVs through fall paralleled increases in deer weight and improved nutritional status. The elevations in Hb and RBC counts occurred despite the potential dilution effect of a second peak in plasma volume (Jacobsen 1978).

In association with minimum seasonal weights during September, white-tailed deer collected in southern Texas exhibited a mean Hb concentration (11.9 g/dL), RBC count (10.8 × $10^6/\mu$L), and PCV (33.0%) (Kie et al. 1983; cf. Table 1) similar to values for these characteristics in our deer while they were at their lowest weight in May (Fig. 3). Greater Hb concentration (19.0 g/dL), PCV (49.0%), and MCV (36.3 fL) in captive white-tailed does fasted for 4 weeks (February–March) (DelGiudice et al. 1987) than in our free-ranging deer during late winter indicated less severe dehydration and milder erythropoetic response to undernutrition in the latter.

White blood cell counts were within the range reported for white-tailed deer (Seal et al. 1981). Anderson et al. (1970) reported seasonal variation in total leukocytes in free-ranging mule deer (*O. hemionus*) in Colorado; highest values occurred during summer (3.6 × $10^3/\mu$L).

Serum characteristics

Several serum characteristics directly associated with nitrogen metabolism exhibited seasonal patterns that conformed with the seasonal variation in deer condition. Seasonal weights and hematological indicators of condition showed that these deer were in peak nutritional condition during October and in poorest condition from May to July.

Lowest total protein concentrations during late winter – early spring were indicative of the net degradation of endogenous protein that accompanies fat mobilization in chronically undernourished deer (Torbit et al. 1985; DelGiudice et al. 1990*a*). Generally similar patterns of total protein values and weight changes seemed to agree with the direct relationship we observed between percent weight and body protein loss in captive deer (DelGiudice et al. 1990*a*). Bahnak et al. (1979) reported diminished total protein and dramatically increased urea N values (>30 mg/dL) in captive white-tailed does that were chronically undernourished during winter, then fasted for a week in April. Hypoproteinemia is also common in domestic species that are protein-malnourished (Kaneko 1989). In free-ranging adult white-tailed deer of the Texas Gulf Prairies, total protein values did not vary seasonally (Kie et al. 1983). However, in less humid central Texas, total protein values were influenced by season, being lowest in October (5.9 ± 0.2 g/dL) and elevated during June (7.2 ± 0.2 g/dL), when ruminal crude protein content was highest (Waid and

Warren 1984). The monthly increase in total protein to maximum values by fall, when our deer were heaviest, indicated the repletion of body protein.

The monthly pattern of urea N concentration provided additional evidence of the seasonal dynamics of protein metabolism in our deer. The progressive increase in urea N concentration (13.1−30.4 mg/dL) that accompanied diminishing deer weights from February to May, and decreased availability and (or) quality of nutrition during most of that time, further indicated steadily accelerating net catabolism of body protein. The trend in urea N concentration in our deer in winter contrasted with the pattern observed in captive white-tailed does undernourished during winter (DelGiudice et al. 1990*a*). In the captive animals, urea N concentration declined to 10.1 ± 2.0 mg/dL after a mean loss of 12.8% of base-line weight, which included 13 and 85% depletion of endogenous protein and fat reserves, respectively (DelGiudice et al. 1990*a*). The difference suggested greater nutritional (i.e., dietary energy) deprivation and energy deficit of the wild deer (Forbes 1985; Torbit et al. 1985), which was probably exacerbated by the increased energetic costs of securing food and moving through snow (Moen 1976). We have reported an increasing effect of starvation on urea N concentration in captive deer (DelGiudice et al. 1987). Morris and Bubenik (1983) presented a monthly pattern of mean urea N values for captive castrated male white-tailed deer similar to ours; however, values in their deer tended to be greater during most of the year.

A serum urea N concentration ≥20 mg/dL in northern deer subsisting on natural vegetation during winter is considered suggestive of severe energy deprivation (DelGiudice and Seal 1988). However, the occurrence of spring greenup during late May in our study area and the resulting direct influence of increased protein intake on urea N concentration must also be considered (Kirkpatrick et al. 1975; DelGiudice et al. 1990*a*). Nevertheless, the decline in urea N concentration in our deer from May to October, when their weight peaked, suggested a positive N balance, decreased body protein catabolism, increasing energy consumption (also indicated by increasing T_3 values), and more efficient metabolism of dietary protein and urea N for net anabolism of body protein. In Texas deer, Waid and Warren (1984) associated elevated urea N concentrations during August with depressed weights and fat reserves. One of their lowest mean urea N values (9.8 ± 1.5 mg/dL) occurred during January, when fat reserves were greatest.

The close similarity between the patterns of monthly creatinine concentrations and weight is also noteworthy. Creatinine production is proportional to muscle mass; thus, the decreasing trend in creatinine concentration from late winter to July, and the subsequent increase through October, were probably primarily atrributable to the parallel trends of muscle mass associated with progressive weight loss and gain, respectively (Torbit et al. 1985; DelGiudice et al. 1990*a*). Morris and Bubenik (1983) observed a similar seasonal trend in intact male deer; however, monthly weights were not presented.

Dehydration and reduced glomerular filtration pressure associated with nutritional deprivation may have an increasing effect on creatinine concentration (Benjamin 1981, p. 178) and may also partially explain the higher creatinine values during late winter than in spring. Increased creatinine concentrations have been associated with moderate nutritional deprivation and weight loss in captive deer during winter, followed by decreased values with spring refeeding (DelGiudice et al. 1990*a*).

In northern deer, transition to a "semi-hibernation state" during late fall is characterized by decreased movement, feeding, thyroid activity, and metabolism (French et al. 1955; Rongstad and Tester 1959; Silver et al. 1969; Seal et al. 1972). The pronounced decline in the urea N : creatinine ratio through fall indicated this seasonal shift in metabolic physiology. Similarly, in black bears (*Ursus americanus*), the urea N : creatinine ratio declines to ≤10.0 during winter dormancy (Nelson et al. 1984; Franzmann and Schwartz 1988; Hellgren et al. 1990). However, the unique physiology of black bears during dormancy enables them to preserve protein (Nelson et al. 1975; Lundberg et al. 1976), whereas chronically undernourished or starving deer catabolize protein for energy (Torbit et al. 1985; DelGiudice et al. 1990*a*). In our deer, the proportional increase in urea N was more responsible than the decline in creatinine concentrations for the increase in urea N : creatinine ratios from winter to spring.

Triiodothyronine is the metabolically active form of the thyroid hormone (Kaneko 1989) and is more sensitive to dietary energy than T_4 (Seal et al. 1978*a*; Bahnak et al. 1981; DelGiudice et al. 1990*a*). The steady elevation in T_3 values from April to September strongly indicated a progressive increase in energy consumption. Positive effects of increased T_3 include increased metabolic rates, positive N balance (i.e., net protein synthesis), and increased erythropoesis (Kaneko 1989). Increased serum T_3 also directly affects glucose absorption and turnover and fertility (Kaneko 1989). Maximum T_3 concentrations occurred close to the rutting season of our deer. The acute drop in T_3 concentration during October, which remained depressed throughout winter, was indicative of the diminished dietary energy available and consumed.

Serum T_3 values did not vary seasonally in free-ranging adult does in Ontario, but an apparent peak occurred in summer (Hamr and Bubenik 1990). Seasonal variation in T_3 values has been noted in captive reproductively intact male deer fed a pelleted ration and natural food supplements year-around, maximum concentrations occurring during December−February (Bubenik and Leatherland 1984). Serum T_3 concentrations during February−March in our deer were comparable to values reported for captive adult does fasted for a week in April after being "semi-starved" all winter (Bahnak et al. 1981).

The absence of a clear seasonal pattern in T_4 concentrations has been previously reported for captive male and female deer (Bubenik and Bubenik 1978; Bubenik and Leatherland 1984) and free-ranging does (Hamr and Bubenik 1990). Furthermore, T_4 concentrations did not vary seasonally in a 2-year study of free-ranging white-tailed does in Oklahoma; however, T_3 concentrations there peaked in fall (DeLiberto et al. 1989).

Compared with conventional techniques of deer capture, the capture collar we used minimizes stress (DelGiudice et al. 1990*b*); thus, we found low cortisol concentrations year-around. That lower cortisol values appeared to occur during late fall and winter than in the May−October period suggested that the declining nutritional state, reduced metabolism, and lower energy intake (as reflected by diminished T_3 concentrations) of these animals during the former period contributed to a less excited response to capture. Bubenik and Leatherland (1984) observed a bimodal pattern of serum cortisol in cas-

trated captive mule deer, with peaks occurring during April and October, and similarly suggested that the spring peak might be due to greater excitability during that time of year. Comparisons of our findings with those from other studies are difficult because of differences in experimental factors (sex, diet, energy budget, degree of stress associated with different immobilization and handling procedures, reproductive manipulation); however, with the use of capture collars, we believe that values in our deer may be most reflective of a seasonal rhythm in free-ranging deer.

Congruent with our other findings, the most probable cause of hyperkalemia during early and late winter was a partial renal shutdown associated with reduced circulatory fluid or decreased plasma volume (Jacobsen 1978; Carlson 1989). The elevated serum creatinine concentrations of February–March indicated a decrease in glomerular filtration during late winter. Considering the disparity in our deers' mean weight between late winter – spring months and fall, extensive muscle wasting may have contributed to the hyperkalemia as well (Carlson 1989). Hypokalemia has been associated with prolonged starvation of captive deer (DelGiudice et al. 1987). Stable potassium concentrations, within the normal range for deer (Seal et al. 1981) during spring, summer, and fall, indicated that our deer were recovering nutritionally. Elevated urinary potassium : creatinine ratios during late March have indicated that deer in our area increase their intake of potassium at that time (DelGiudice et al. 1989*b*).

Seal et al. (1978*b*) reported a lower serum potassium level (4.4 ± 0.1 mequiv./L) than in this study for adult deer in the same area during winter and early spring. In Colorado, serum potassium levels in mule deer were highest in spring and summer, when the potassium content of plants was highest (Anderson et al. 1972; Short et al. 1966). Elevated serum potassium values have also occurred in Oklahoma white-tailed deer during spring and summer (9.5–11.2 mequiv./L) (DeLiberto et al. 1989). Serum potassium values of white-tailed deer in Texas were somewhat higher (means 7.7–8.29 mequiv./L) than in our deer, but values did not vary seasonally (Kie et al. 1983; Waid and Warren 1984).

This study was not designed to examine the effects of pregnancy on serum indicators of physiologic and metabolic status. Presumably, the most apparent effects of gestation occur during the last trimester as the fetus gains greatest mass, and the energetic costs to the doe increase towards term (Robbins 1983, p. 172). Several of our does were pregnant, as evidenced by the presence of fawns or by lactation during late May or July; however, observations were not conclusive for all does handled.

Findings by others of such effects have been inconsistent and inconclusive (Seal et al. 1972; Bahnak et al. 1979, 1981; Kie et al. 1983; Waid and Warren 1984). Comparing the results of different studies is difficult because of the varying magnitude of dietary stress of study animals throughout gestation, as well as before pregnancy. A rigorously controlled serial examination of the potential influence of gestation on serum characteristics is warranted.

Fluctuations in the quantity and quality of deer nutrition are associated with wide seasonal variations in weather on northern ranges. These variations were clearly reflected in our deer by weight trends that included 30.2% lower mass in May than in October. The seasonal changes in metabolic physiology that permit deer to survive such variations in weight and overall condition were reflected by patterns of hematological characteristics and serum metabolites, hormones, and electrolytes. The shift in metabolism was partially attributable to an endogenous rhythm (Silver et al. 1969), but the intensity of its expression was most likely affected by nutrition (Bahnak et al. 1981). Year-to-year changes in the seasonal trends of deer hematologic profiles and serum characteristics may be useful to investigations of specific nutritional effects of environmental vagaries, progressive habitat changes, reproduction and survival, and population changes.

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