

Influences of winter supplemental feeding on the energy balance of white-tailed deer fawns in New Hampshire, U.S.A.

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Abstract: The purpose of this study was to determine the influence of supplemental feeding on the energy balance of white-tailed deer (*Odocoileus virginianus*) in northern New Hampshire, U.S.A., during January–March 1997. We measured the field metabolic rate (FMR) and energy balance of 10 (5 males and 5 females) supplementally fed wild fawns with doubly labeled water over 19–21 days. We tested whether percent acid detergent fiber (ADF) and percent neutral detergent fiber in deer fecal samples predicted the proportion of supplemental feed (pelleted concentrate) in the diet of deer. The mean FMR of fawns was $758.4 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ (range = $535.9\text{--}1032.8 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$), or $2 \times$ their basal metabolic rate (BMR). The mean FMR of male fawns was $>30\%$ higher than that of female fawns. Percent body fat ($12.1 \pm 1.4\%$ (mean \pm SE)) and mass loss ($3.0 \pm 0.9\%$) varied among fawns, suggesting that an individual high FMR was not detrimental to energy balance and was related to availability of feed. We estimated that a high FMR ($>2 \times$ BMR) could be maintained only if fawns consumed about 1 kg of supplemental feed daily. Radiotelemetry data indicated that the number and juxtaposition of feeding sites in an area probably influenced home range and activity of deer. Percent ADF in feces provided the best prediction of percent grain in the diet ($\% \text{ grain} = -0.048(\% \text{ ADF})^2 + 1.523(\% \text{ ADF}) + 96.467$; $r^2 = 0.69$) and was useful for identifying populations consuming supplemental pelleted concentrate. Biologists should expect that the influence of winter feeding on energy balance and survival will vary according to the interrelationships of deer density, food availability, and winter severity at feeding sites.

Résumé : Nous avons tenté de déterminer l'influence que peut avoir un supplément de nourriture sur l'équilibre énergétique chez le cerf de Virginie (*Odocoileus virginianus*), dans le nord du New-Hampshire, É.-U., de janvier à mars 1997. Nous avons mesuré le taux de métabolisme (FMR) et l'équilibre énergétique en nature chez 10 faons (5 mâles et 5 femelles) qui ont reçu de l'eau doublement marquée pendant une période de 19–21 jours. Nous avons vérifié si le pourcentage de fibres détergentes acides (ADF) et le pourcentage de fibres détergentes neutres dans les fèces des cerfs permettent de prédire la proportion de nourriture en supplément (boulettes de nourriture concentrée) dans le régime des cerfs. Le taux de métabolisme FMR moyen des faons s'élevait à $758,4 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{j}^{-1}$ (étendue de $535,9$ à $1032,8 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{j}^{-1}$), soit 2 fois leur taux de métabolisme de base (BMR). Le taux FMR moyen était plus de 30 % plus élevé chez les faons mâles que chez les faons femelles. Le pourcentage de graisses corporelles ($12,1 \pm 1,4 \%$ (moyenne \pm écart type)) et la perte de masse ($3,0 \pm 0,9 \%$) étaient variables, ce qui veut dire qu'un métabolisme FMR élevé chez un individu n'a pas d'influence négative sur son équilibre énergétique et est relié à la disponibilité de la nourriture. Nous avons estimé que pour que son métabolisme FMR soit élevé ($>2 \times$ BMR), un faon doit consommer au moins 1 kg de nourriture supplémentaire par jour. Les données radio-téléométriques indiquent que le nombre et la juxtaposition des sites d'alimentation dans une région influencent probablement le domaine et l'activité des cerfs. Le pourcentage de fibres ADF dans les fèces est le meilleur facteur de prédiction du pourcentage de grain dans le régime ($\% \text{ grain} = -0,048(\% \text{ ADF})^2 + 1,523(\% \text{ ADF}) + 96,467$; $r^2 = 0,69$) et cette valeur a permis d'identifier les populations qui avaient reçu des boulettes de concentré en supplément. Les biologistes doivent s'attendre à ce que l'influence de l'alimentation d'hiver sur l'équilibre énergétique et sur la survie varie en fonction des interrelations entre la densité des cerfs, la disponibilité de la nourriture et la rigueur de l'hiver aux sites d'alimentation.

[Traduit par la Rédaction]

Introduction

Winter feeding

White-tailed deer (*Odocoileus virginianus*) near the northern limit of their geographic range are frequently exposed to extreme winter conditions of deep snow and low tempera-

tures that reduce food availability and increase the energetic cost of foraging and thermoregulation (Moen 1976). The low digestibility of winter browse typically reduces forage intake below the maintenance energy requirement of deer (Mautz et al. 1976; Gray and Servello 1995). Deer compensate for low energy intake by catabolizing fat and protein

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tissue and reducing activity (Ozoga and Verme 1970; Moen 1976, 1978), survival being dependent upon balancing energy derived from tissues and forage with seasonal energy costs. When winter conditions severely limit browse availability, diets such as pelleted concentrates may allow deer to increase their forage and energy intake, which may reduce winter mortality (Hobbs 1989). Although wildlife professionals generally consider winter feeding of deer an unnecessary or unwise practice (Olsen and Lewis 1994), supplemental high-energy, high-protein feed can increase winter survival of local deer herds (Mautz 1983; Baker and Hobbs 1985; Hobbs 1989).

Providing high-quality food supplements to wintering white-tailed deer is a popular practice among private citizens and sportsmen's groups in the northeastern United States and Canadian provinces. It will likely increase as humans further reduce the amount of available deer habitat without changing their demand for large deer populations (Hubert et al. 1980; Ozoga and Verme 1982). Although the New Hampshire Fish and Game Department does not advocate feeding deer in winter, biologists estimate that more than half of the deer in northern New Hampshire use wintering areas in close proximity to supplemental feeding sites.

Supplemental winter feeding can directly influence the energetic and nutritional status of free-ranging deer by reducing mass loss (Ozoga and Verme 1982; Carpenter et al. 1984; Boutin 1990) and increasing fawn survival (Verme and Ozoga 1980). A high-energy, high-protein diet provided in late winter or early spring may also allow malnourished deer to replace endogenous protein that has been catabolized during winter (Ozoga and Verme 1982; DelGiudice et al. 1990). Supplemental winter feeding may also increase productivity of a deer herd, provided feed is consumed by a large portion of the deer population (Robinette et al. 1973; Carpenter et al. 1984). Fawns fed high-energy diets may reach sexual maturity at a younger age (Abler et al. 1976; Ozoga and Verme 1982; Ozoga 1988), overall fawn production may increase (Ozoga and Verme 1982), and mortality of newborn fawns may be reduced (Carpenter et al. 1984).

Although it seems intuitive that deer would benefit from supplemental winter feeding, some deer herds are negatively impacted or show no change in population dynamics after the addition of a high-quality food source (Robinette et al. 1973; Dean 1976; Ozoga and Verme 1982; Lenarz 1991). Additionally, supplemental feeding may alter movement and yarding patterns of wintering deer (Boutin 1990; Schmidt and Gossow 1991; Easton 1993), and many emergency feeding programs have failed to reduce deer mortality during severe winters (Carhart 1943; Doman and Rasmussen 1944; Dean 1976; Baker and Hobbs 1985).

Deer density at supplemental feeding sites generally increases as winter progresses, creating a situation in which high-quality feed may become a limiting resource (Schmitz 1990). Although fawns are the segment of the deer population that presumably benefit most from supplemental feed, they are generally excluded from feeding sites by larger, dominant deer (Ozoga 1972; Schwartzkopf 1990; Easton 1993). As a result, fawns may experience increased mass loss when deer density at feeding sites is high (Ozoga and Verme 1982).

Although most wildlife agencies in northeastern North America acknowledge that supplemental feeding of deer is

prevalent and increasing, few, if any, collect quantitative data regarding the energetic effects of supplemental feeding on their resident deer herds. Therefore, our goal was to assess how supplemental feeding influences the winter energy balance of deer. Specifically, we measured energy expenditure, energy balance, activity levels, and movement patterns of free-ranging deer utilizing supplemental feed.

Study area

This study was conducted during January–March 1997 in Coos County, New Hampshire, primarily in the town of Pittsburg located at 45°0'N, 71°30'W on the Canadian border. Most of the forest land was commercially owned and managed, and the mature softwood in the deer wintering areas had been harvested extensively since 1975. Dominant forest types in this area were saw-timber spruce–fir and northern hardwoods including balsam fir (*Abies balsamea*, 25%), red spruce (*Picea rubens*, 20%), yellow birch (*Betula alleghaniensis*, 14%), sugar maple (*Acer saccharum*, 13%), paper birch (*Betula papyrifera*, 6%), red maple (*Acer rubrum*, 5%), and aspen (*Populus* spp., 4%) (Frieswyk and Malley 1985). February is typically the coldest month of the year, averaging -13°C ; average annual snowfall was 414 cm (Owenby and Ezell 1992).

Deer were captured in Pittsburg at two primary study sites where supplemental feed (pelleted concentrate, hereinafter “grain”) was provided. The first study site (River Road) encompassed four supplemental feeding sites (“fed sites”) where grain was provided at least once daily. Additionally, three other landowners in this area provided grain periodically throughout winter. All fed sites at River Road were situated within 1 km² area inside a historic deer wintering area that had been fragmented by private residences (12/km²). The second study site (Route 3) encompassed three fed sites where grain was provided at least once daily. All fed sites at Route 3 were located on the periphery of a 6-km² deer wintering area.

Eight additional fed sites and four traditional wintering areas without supplemental feed (“unfed sites”) were used to collect comparative data within a 50-km² area. Sites were chosen on the basis of their traditional use and proximity to the nearest known supplemental feeding site. A complete description of all fed and unfed sites is provided in Tarr (1999).

Materials and methods

We hypothesized that deer consuming supplemental food as a significant portion of their diet have different energy budgets than deer consuming only winter browse. Therefore, to determine the influence of winter supplemental feeding on deer energy balance, we measured the energy expenditure, body composition, movement, and home range of deer at fed sites and compared the proportions of supplemental feed predicted in the diet of deer at fed and unfed sites. All animal-care and experimental procedures were approved by the University of New Hampshire Animal Care and Use Committee (No. 960602).

Consumption of supplemental feed

Since typical winter-browse diets have a significantly higher fiber content than most commercially manufactured

deer concentrates (Short et al. 1974; Mautz et al. 1976; Pekins and Mautz 1988), measurement of the percentage of fiber in deer fecal pellets may provide a method of identifying supplementally fed deer herds. Although the efficacy of using fecal fiber to predict deer diet composition had not been investigated, we hypothesized that deer consuming low-fiber supplemental food would have a substantially lower percentage of fecal fiber than deer consuming diets consisting only of high-fiber woody browse.

Captive deer

Captive deer at the University of New Hampshire Wildlife Research Facility were used to develop predictive equations between the percentage of fecal fiber and the dietary proportion of supplemental feed (percent grain). During February 1997, five female fawns were fed diets consisting of known proportions of winter browse (0–100%) and grain to simulate diets of wild deer visiting supplemental-feeding sites. The winter-browse portion consisted of a mixture of typical winter forages relatively high in fiber and low in protein, including annual growth of red maple, northern red oak (*Quercus rubra*) acorns, senesced northern red oak leaves, and northern white cedar (*Thuja occidentalis*). The dietary proportions were set at 0, 25, 50, 75, and 100% winter browse, with the remainder of the diet equal to grain. The grain contained 8% crude fiber and was the maintenance ration of the captive herd (UNH deer feed, Agway, Inc., Syracuse, N.Y.).

Deer were fed individually in 4 × 5 m pens and gradually acclimated to browse for 2–3 weeks. Each received 1–2 kg of food daily depending upon their individual consumption pattern. Daily consumption of browse was increased steadily by reducing available grain. Deer eventually received 100% browse for 7–10 days, followed by fecal collection for 3 consecutive days. The amount of grain was then increased in a progressive manner to produce fecal samples for the prescribed portions. Fecal samples were collected for 3 days after 2–3 consecutive days of stable intake at each proportion. Because deer were sometimes selective in their consumption patterns, the actual proportions of browse to grain consumed were determined through measurement of daily orts. All fecal samples were frozen immediately.

Diet and fecal samples were dried and ground in a Wiley Mill (1 mm mesh screen). These samples were analyzed for percent neutral detergent fiber (NDF) and percent acid detergent fiber (ADF) via standard laboratory procedures at the Colorado State University Range Science Laboratory. Linear and curvilinear regression analyses were used to examine the relationships of percent NDF and percent ADF with percent grain in the diet.

The body composition of the five captive fawns was measured by dilution of deuterium oxide ($^2\text{H}_2\text{O}$) in body water (Rumpler et al. 1987; Worden and Pekins 1995). Each fawn was weighed to the nearest kilogram and immobilized with 30–50 mg of xylazine hydrochloride (100 mg/mL). A baseline blood sample (5 mL) was drawn from the lateral saphenous vein, and each animal received 0.15 g $^2\text{H}_2\text{O}$ /kg body mass (99.9% at. excess). After equilibrium (approximately 4 h), a second blood sample was collected. Each fawn received 0.11 mg yohimbine/kg body mass (2 mg/mL) to reverse the

effects of xylazine. Isotope concentrations in blood plasma were measured by isotope mass spectrometry (Metabolic Solutions, Inc., Merrimack, N.H.). Total body water was calculated as in Worden and Pekins (1995). Estimates of total body water were converted to ingesta-free body-water content with the equations of Robbins et al. (1974) and Torbit et al. (1985).

Wild deer

Fecal samples were collected monthly from 8 January to 20 March at each of the eight fed sites, including the four sites where study fawns were captured at River Road and Route 3. Whenever possible, fecal samples were collected from deer of known age and sex (i.e., adult male, adult female, fawn), and the remainder were collected as “random” samples from unknown deer. Fecal samples were also collected at each of the four unfed sites; they were considered random samples because we seldom observed deer at unfed sites.

Sampling was done within 3 days of the most recent snowfall ≥ 8 cm in order to best approximate fecal deposition date. Fecal samples were stored frozen and were prepared and analyzed as described for captive deer. Mean monthly and mean winter values were calculated for each site. These values were used in the predictive equations developed using captive deer to estimate percent grain consumed by deer at each site. Analysis of variance and the Tukey–Kramer honestly significant differences method (Systat[®] 7.0, SPSS, Inc., Chicago) were used to test for differences ($P < 0.05$) between months, fed and unfed sites, and age and sex classes of deer.

Energy expenditure

Energy expenditure, body composition, and home ranges of 10 wild fawns (5 males and 5 females) were measured during January–March 1997. Fawns were captured at two sites at both River Road and Route 3 by darting with 0.75 mL of 100 mg xylazine + 250 mg Telazol[®]/mL delivered in a 1-cm³ Pneu-dart[®]. Fawns were darted over grain piles at distances of 25–36 m.

Each deer was sexed, weighed, ear-tagged, radio-collared (expandable MOD-500 radio collars, Telonics, Inc., Mesa, Ariz.), and injected intramuscularly with doubly labeled water (0.19 mL/kg body mass; 99.9% deuterium (^2H) enrichment, 90% (^{18}O) enrichment). Blood samples (10 mL) were collected prior to injection of doubly labeled water and after isotopic equilibration with body water (approximately 4 h). After injection, fawns were placed in a darkened crate to minimize disturbance and excitement upon arousal. Each received 50 mg of xylazine about 30 min before the second blood sample was collected, after which each received 0.11 mg yohimbine/kg body mass (2 mg/mL) to reverse the effects of the xylazine. Subsequent release took place at the capture site after each stood and became active within the holding crate. Fawns were recaptured 19–21 days later at fed sites by darting with the xylazine–Telazol[®] mixture. Each was weighed, blood-sampled (10 mL), and subsequently released as described for the initial capture.

Isotopic concentrations in blood plasma were measured by isotope-ratio mass spectrometry (Metabolic Solutions, Inc., Merrimack, N.H.). Total body water and body composition

were calculated as described previously for captive fawns. The rate of CO₂ production was calculated for each fawn by the two-point method: the rate of ²H and ¹⁸O loss (*k_d* and *k_o*, respectively) was determined as the difference between isotope enrichments in blood samples collected at the time of capture and at recapture. We calculated CO₂ production with the one-pool doubly labeled water equations used by Fancy et al. (1986) to validate the technique in caribou (*Rangifer tarandus granti*). Calculations of CO₂ production were corrected to account for errors associated with ²H incorporation into methane (CH₄) and in exchangeable and non-exchangeable sites in feces (Midwood et al. 1989, 1993, 1994). A full description of the calculations made for this study is provided in Tarr (1999).

Total CO₂ production of deer was converted into total energy expenditure by multiplying the volume of CO₂ produced by the caloric equivalent (24.41 kJ/L CO₂) of the respiratory quotient (RQ) 0.83. Gessaman and Nagy (1988) calculated that using a RQ of 0.83 produces minimal (±3%) error when the RQ of a herbivore is unknown.

Home range

Activity and movement of each deer were monitored at least twice daily with radiotelemetry. Locations were plotted immediately on a U.S. Geological Survey topographic map after triangulation of two or three radio signals. Because most locations of a single individual were autocorrelated, home ranges were constructed with minimum convex polygons following the recommendation of Swihart and Slade (1985). Minimum convex polygons were constructed using the program McPaal, which estimated home ranges to the nearest 0.1 km².

Weather

A weather station was placed proximate to a feeding site at River Road and at Route 3 to measure ambient temperature (°C) and wind speed (m/s). Ambient temperature and wind speed were measured every 60 s at each station and averaged every 15, 60, and 1440 min (24 h). Each weather station consisted of a CR-10 datalogger (Campbell Scientific Inc., Logan, Utah) that continuously monitored voltage signals from a temperature probe and anemometer positioned at 2 m height. Both stations were placed under softwood canopy within areas that deer frequented daily. Daily and period averages were calculated for the study period for each deer. Analysis of variance was used to test for differences (*P* < 0.05) in weather experienced by deer between time periods (January – early February, mid-February, late February – March) and capture sites (River Road and Route 3). Regression analysis was used to test for a relationship between ambient temperature and field metabolic rate (FMR).

Results

Consumption of supplemental feed

Thirty fecal samples were obtained from five captive fawns that consumed mixed rations of grain and natural browse; 15 samples occurred within a dietary range of 22–72% browse. The range of values for fiber was 50.0–82.9% ADF and 26.8–64.0% NDF. Significant linear and curvilinear relationships

Table 1. Mean ADF and percent grain measured in fecal samples from white-tailed deer (*Odocoileus virginianus*) collected at fed and unfed sites in northern New Hampshire in January–March 1997.

Site*	<i>n</i>	% ADF	% grain
Fed sites			
FED1	16	52.7 ± 1.1	42.4 ± 3.8 <i>a</i>
FED2	13	49.3 ± 2.2	52.2 ± 6.8 <i>bc</i>
RT31	26	55.1 ± 1.0	33.4 ± 3.6 <i>ac</i>
RRD1	27	51.5 ± 1.0	46.2 ± 3.6 <i>acd</i>
RT32	12	49.8 ± 1.4	52.0 ± 4.8 <i>bc</i>
FED3	10	58.1 ± 2.0	21.1 ± 7.5 <i>bd</i>
RRD2	22	54.6 ± 0.8	35.8 ± 2.9 <i>bd</i>
FED4	11	48.9 ± 1.4	55.1 ± 5.0 <i>acd</i>
Combined	137		41.6 ± 1.7 [†]
Unfed sites			
UF1	12	56.4 ± 0.7	29.5 ± 2.7 <i>a</i>
UF2	15	57.3 ± 1.0	25.3 ± 4.1 <i>ac</i>
UF3	8	57.4 ± 1.6	24.7 ± 6.4 <i>ac</i>
UF4	16	60.5 ± 0.9	12.2 ± 3.6 <i>bc</i>
Combined	51		22.1 ± 2.2

Note: Percent grain was estimated using the following equation: % grain = -0.048(% ADF)² + 1.523(ADF) + 96.467. Values in rows followed by a different letter are significantly different (*P* < 0.05).

*FED, sites not located at either River Road or Route 3; RT3, Route 3 fed sites; RRD, River Road fed sites.

[†]Significant difference between combined means of percent grain at fed and unfed sites (*P* < 0.05).

existed between percent grain in the diet and both percent NDF and percent ADF:

$$[1] \quad \% \text{ grain} = -3.52(\% \text{ NDF}) + 293.04; r^2 = 0.62, \\ P = 0.001, F = 72.07$$

$$[2] \quad \% \text{ grain} = -0.072(\% \text{ NDF})^2 + 6.06(\% \text{ NDF}) \\ - 18.0156; r^2 = 0.64, P = 0.001, F = 49.809$$

$$[3] \quad \% \text{ grain} = -2.897(\% \text{ ADF}) + 191.623; r^2 = 0.62, \\ P = 0.001, F = 85.53$$

$$[4] \quad \% \text{ grain} = -0.048(\% \text{ ADF})^2 + 1.523(\% \text{ ADF}) \\ + 96.467; r^2 = 0.69, P = 0.001, F = 59.07$$

The best relationship (eq. 4; *r*² = 0.69) was used to evaluate whether differences existed in percent grain in the diet of wild deer at fed and unfed sites, among sites within a feeding category, and among months. The predicted percent grain in deer diets was higher (*P* = 0.001) at fed (41.6 ± 1.7% (mean ± SE)) than at unfed (22.1 ± 2.2%) sites (Table 1). For all fed sites except FED3, mean percent grain in the diet was ≥33%; for all unfed sites, mean percent grain was ≥30% (Table 1). Mean percent grain in the diet of deer at River Road (39.6 ± 3.6%) was similar to that at Route 3 (41.5 ± 2.4%) (*P* = 0.65).

There were no differences in percent grain in the diet between deer age/sex classifications. However, percent grain in the diet of random deer (39.0 ± 2.1) was lower (*P* = 0.03) than in that of adult males (54.0 ± 4.7). No monthly variation existed (*P* = 0.48) in the amount of grain in diets at fed sites (range = 39.7 ± 2.7 to 43.2 ± 2.7%) or unfed sites (range =

Table 2. Body mass, total body water, and estimated body fat of 10 fawns measured with doubly labeled water during winter 1997, Pittsburg, N.H.

Deer ID No.	Dates	Mass (kg)	Mass loss		Body water (%) ^a	Body fat ^a	
			kg	%		kg	%
F1	17 Jan. – 7 Feb.	34.0	1.0	3.0	60.0	5.2	15
M1	17 Jan. – 7 Feb.	40.0	0	0	60.5	5.8	15
M2	17 Jan. – 7 Feb.	33.5	+1.0	5.0	63.0	4.0	12
M3	27 Jan. – 15 Feb.	37.8	0.5	1.5	65.9	3.3	9
F2	28 Jan. – 17 Feb.	32.3	2.7	8.0	57.9	5.7	17
M4	7–28 Feb.	40.2	1.4	3.4	59.9	6.2	15
F3	8–23 Feb.	33.6	0	0	60.0	5.1	15
F4	17 Feb. – 9 Mar.	30.7	0.4	1.3	71.5	0.9	3
M5 ^b	17 Feb.	33.5	na	na	67.6	2.3	7
F5	18 Feb. – 9 Mar.	40.0	1.8	4.4	62.4	5.1	13
Mean ± SE		35.6 ± 1.13	0.7 ± 0.4	3.0 ± 0.9	62.9 ± 1.3	4.3 ± 0.5	12.1 ± 1.4

^aBased on inješta-free body mass estimated at the beginning of each study period.

^bFawn was not recaptured.

Table 3. Dilution spaces of ²H (N_d) and ¹⁸O (N_o), fractional turnover rates of ²H (k_d) and ¹⁸O (k_o), and $N_d:N_o$ ratios measured in nine supplementally fed fawns during winter 1997, Pittsburg, N.H.

Deer ID No.	Mass (kg)	N_d (mol)	N_o (mol)	k_d (mol/d)	k_o (mol/d)	$N_d:N_o$
F1	34.0	1230.60	1226.60	-0.10767908	-0.136257766	1.003
M1	40.0	1478.52	1396.05	-0.08963178	-0.118415553	1.059
M2	33.6	1275.91	1156.73	-0.10777515	-0.154055694	1.103
M3	37.8	1536.89	1418.51	-0.10179645	-0.139588427	1.083
F2	32.3	1194.57	1128.24	-0.09161586	-0.117618770	1.059
M4	40.2	1465.40	1444.79	-0.12767157	-0.145187014	1.014
F3	33.6	1226.17	1190.36	-0.09647963	-0.118948940	1.030
F4	30.7	1263.25	1248.12	-0.08220527	-0.105365773	1.076
F5	40.0	1606.25	1437.85	-0.07176759	-0.109673723	1.117
Mean ± SE						1.066 ± 0.013

15.2 ± 4.7 to 25.9 ± 2.9%). Percent grain predicted from fecal samples ($n = 17$) from fawns treated with doubly labeled water ranged from 42.6 ± 8.2 (mean ± SE) (fawn M2) to 59.6% (fawn F1).

Energy expenditure

The mean ambient temperatures during measurement periods for individual deer ranged from -5.0 to -13.6°C. The lowest temperature measured was -29.6°C, with temperature variations of 15–20°C within any study period. Wind speed was negligible in all periods, as average daily wind speed was never >1.0 m/s. Precipitation within a study period was low to moderate, ranging from 17.8 to 63.5 cm snow. Snow depth rarely exceeded 60 cm and deer movements were concentrated on packed trails leading to fed sites.

Ten fawns (5 females and 5 males) were captured at fed sites on River Road and Route 3 during January and February; 9 were recaptured 19–21 days later. Initial body mass of these deer ranged from 30.7 to 40.2 kg. Male fawns were not larger than female fawns ($P = 0.22$) but, on average, were 2.9 kg heavier (Table 2). Six fawns lost mass during the study (0.5–2.7 kg, 1.5–8% body mass), two (M1 and F3) maintained mass, and one (M2) gained 1.8 kg at River Road (Table 2). No fawn died during the study; the single fawn not recaptured (M5) visited the capture site irregularly after its initial release. All attempts to recapture this fawn in the

field were unsuccessful, and it subsequently dispersed from Pittsburg in late March.

Estimated percent body fat at initial capture was highly variable (3–17%) (Table 2) but did not differ between males and females ($P = 0.77$) or between the River Road and Route 3 capture sites ($P = 0.31$); however, the value at River Road (14.2 ± 0.6) was >1.5 times that at Route 3 (9.7 ± 4.3). Percent body fat did not differ among time periods (January, mid-February, and late February; $P = 0.10$), although the average value in late February (7.5%) was about half that measured in the two earlier periods. This value was similar to percent body fat of captive fawns measured in February (8.9 ± 1.0%) after consuming natural browse diets for 4–5 weeks.

Estimates of FMR were obtained for 8 of the 10 deer injected with doubly labeled water; fawn M5 was not recaptured and the isotope concentrations in M4 at recapture (day 21) were too similar to its baseline concentrations, precluding reliable calculation of FMR. We estimated the FMR of each fawn after correcting the calculated CO₂ production for loss of ²H isotopes in CH₄ and feces. Isotope-dilution spaces, isotope-flux rates, and the $N_d:N_o$ ratio for each fawn are presented in Table 3. The $N_d:N_o$ ratio calculated from fawns was 1.066 ± 0.013 (mean ± SE; range = 1.003–1.117) (Table 3).

We used the mean FMR values estimated from the corrected

Table 4. Mean FMRs and FMR:BMR ratios of fawns measured with doubly labeled water, January–March 1997, Pittsburg, N.H.

Deer ID No.	Body mass (kg) ^a	Vol. CO ₂ produced (L/d)	FMR ^b (kJ·kg ^{-0.75} ·d ⁻¹)	FMR:BMR ^c
F1	34.0	393.5	681.2	1.8
M1	40.0	454.5	697.9	1.9
M2	33.5	591.8	1032.0	2.7
M3	37.8	592.9	1161.4	3.1
F2	32.3	335.3	606.2	1.6
F3	33.6	307.2	535.5	1.4
F4	30.7	329.4	618.4	1.6
F5	40.0	611.0	937.8	2.5
Mean ± SE	35.2 ± 1.3	451.9 ± 45.9	757.8 ± 66.2	2.1 ± 0.2

^aAverage over the study period.

^bEstimated after reducing N_o by 1% to account for the overestimate of N and after adjusting the rate of CO₂ production to account for ²H exchange and sequestration in feces and methane.

^cBMR = 376.8 kJ·kg^{-0.75}·d⁻¹ (Silver et al. 1969; Jensen et al. 1999).

rate of CO₂ production of fawns to test for differences in FMR between the sexes, among winter periods, and between study sites. There was no difference ($P = 0.12$) between the mean FMRs of male and female fawns, although the FMR of males (893.9 ± 100.9 kJ·kg^{-0.75}·d⁻¹ (mean ± SE)) was >30% higher than that of females (675.8 ± 69.5 kJ·kg^{-0.75}·d⁻¹); FMR was 757.8 ± 66.2 kJ·kg^{-0.75}·d⁻¹ (Table 4). The FMR of males ranged from 697.9 to 1032.0 kJ·kg^{-0.75}·d⁻¹ and the ratio of FMR to basal metabolic rate (BMR) (376.8 kJ·kg^{-0.75}·d⁻¹; Silver et al. 1969; Jensen et al. 1999) ranged from 1.9 to 3.1 (Table 4). The FMR of females ranged from 535.5 to 937.8 kJ·kg^{-0.75}·d⁻¹, with the FMR:BMR ratio ranging from 1.4 to 2.5 (Table 4). There was no difference in FMR among winter periods ($P = 0.83$) or between study sites ($P = 0.74$). Regression analysis showed no relationship between ambient temperature and FMR ($P = 0.90$).

Home range

There were 38–59 locations recorded per fawn throughout the 19- to 21-day periods. All fawns returned to their original capture site within 72 h of initial capture, with most returning within 12–48 h. Fawns visited one to four separate fed sites; all fawns at River Road visited at least two sites. The mean home range of fawns at River Road was only 0.2 km² and was smaller ($P = 0.04$) than that at Route 3 (3.7 km²). The smallest and largest home ranges were 0.1 km² (fawn F1, River Road) and 8.2 km² (fawn M5, Route 3).

Discussion

Consumption

The difference in percent ADF in fecal samples from fed and unfed sites indicated that this measurement can identify local deer populations that utilize supplemental feed in the form of pelleted concentrate. Although eq. 4 did not predict 0% grain at unfed sites, the predicted percent grain at fed sites (42.0 ± 1.7 (mean ± SE)) was nearly twice that at unfed sites (25.5 ± 2.0). Values at fed sites were reasonable, as they reflected the general trend in grain availability and deer density at each site; four sites that provided grain at least twice daily had predicted diets with >45% grain. The lack of

monthly differences indicated that deer were present and used supplemental feed extensively throughout the study.

The variability in the predicted percent grain at unfed sites was not expected, although browse quality (i.e., fiber content) varies within deer wintering areas. For example, deer at site UF3 had continuous access to treetops from a logging operation, whereas deer at UF4 wintered at high elevation in deep snow without access to regenerated forest. It is possible that deer at UF1 and UF2 accessed supplemental feed occasionally because FED3, where feed was provided sporadically, was within 3 km. The combination of low grain availability and high deer numbers may explain why the predicted percent grain at FED3 was similar to values at the unfed sites (Table 1).

Differences in predicted percent grain at fed sites were expected because the amount of feed, number of deer, and visitation rates varied among sites. For example, the highest predicted percent grain was at FED4 (55.1 ± 5.0 (mean ± SE)), where about 45 kg of grain was provided daily; conversely, FED3 had feed provided once daily or less. No other site provided >10 kg grain daily. The estimated number of deer visiting any one site ranged from 10 to 45, and multiple daily visits per deer, including certain study deer, were common.

Although the differences were not significant, the percent grain in the diet of adult males (54.0 ± 4.8 (mean ± SE)) was higher than in the diet of adult females (44.2 ± 4.8) and fawns (40.6 ± 5.5), reflecting the expected presence of a dominance hierarchy (Schwartzkopf 1990) and the general feeding order observed at fed sites. Fawns were usually excluded from feeding unless grain was provided in numerous, separated piles. The lower percent grain in random samples (39.0 ± 2.1) was not surprising, given that the observed herd composition at fed sites comprised predominantly adult does and fawns. The percent grain in random samples suggests that the diet predicted from such samples probably represented the typical composition of the sampled herd and that the amount of supplemental food consumed varied among deer.

The relationship between percent ADF in fecal samples and percent grain in the diet differentiated between fed and unfed sites. However, a small change in ADF above 50% yields a relatively large change in the predicted percent grain

in the diet. The relative sensitivity of the equation, coupled with the variance associated with individual deer and ADF measurements, may preclude accurate prediction of differences in grain intake among fed sites. However, it is also possible that the rate of grain consumption at typical fed sites rarely exceeds 40–60% because deer continue to browse regardless of the amount of supplemental feed (Ozoga and Verme 1982; Schmitz 1990). Measuring the extent of supplemental feeding may be limited to identifying relative ranges such as 0–25, 25–50, and >50% grain in the diet.

Energy expenditure

The mean FMR included data from three fawns (M2, M3, and F5) that had FMR:BMR ratios ≥ 2.5 (Table 4). Initially we questioned the validity of the FMR of these three individuals because it would be difficult for fawns to maintain this level of energy expenditure without consuming grain as a large portion of their daily energy intake (see the discussion that follows). If we exclude the FMRs from M2, M3, and F5, the mean FMR was $628.0 \pm 28.9 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ and the FMR:BMR ratio was 1.7 ± 0.1 (mean \pm SE) (range = 1.4–1.9). This mean FMR is within 5% of the metabolizable energy intake (MEI) required for maintenance of captive white-tailed deer fawns ($640.6 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$; Holter et al. 1977) and captive mule deer (*Odocoileus hemionus hemionus*) fawns ($661.5 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$; Baker et al. 1979). Aside from our study, the only other measurement of the FMR of a free-ranging fawn with doubly labeled water was made by Pekins (1995; P.J. Pekins, unpublished data) using a nonsupplementally fed individual released into northern New Hampshire during winter; its FMR ($676.6 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$, FMR:BMR = 1.8) was similar to that measured in our fawns, although its mass loss was much higher.

Previous measurements of maintenance energy requirements and FMR of adult deer also provide insight to the validity of the fawn FMRs (with FMR:BMR < 2.0). The maintenance energy requirement of captive white-tailed does was $549 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ (Ullrey et al. 1970), whereas the winter FMR of released, nonsupplementally fed does in northern New Hampshire was $578 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ (range = 536–620 $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$; Pekins 1995; P.J. Pekins, unpublished data). The similarity between the FMR and maintenance energy requirements of fawn and adult deer likely indicates the basic strategy of energy conservation by white-tailed deer during winter (Moen 1976; Mautz 1978). The higher FMR of fawns reflects their higher BMR and maintenance energy requirements relative to adults. However, the inclusion of M2, M3, and M5 substantially elevated the overall mean FMR of our fawns because their FMRs were about 40% higher than those of the others. It is important to note that the physical condition of all fawns was reasonably similar, indicating that those with the highest FMR did not experience a severe decline in body condition.

The mean FMR measured with doubly labeled water in black-tailed deer (*Odocoileus hemionus sitkensis*) was 648 and 799 $\text{kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ in two consecutive winters in Alaska (Parker et al. 1999). Robbins (1993) suggested that the FMR of wild mammals is generally $>2 \times$ BMR, a value similar to that measured by Parker et al. (1999) in black-tailed deer and our fawns with highest values. However, these values are considerably greater than that measured in our female

fawns and free-ranging, released deer, indicating the energy-conserving potential of white-tailed deer in winter.

Certain factors may have contributed to the elevated FMRs of M2, M3, and M5, including diet quality and consumption rate. Hudson and Christopherson (1985) suggested that the metabolism of animals fed highly nutritious diets is higher than that of animals consuming less nutritious rations. Jensen et al. (1999) found that the resting metabolic rate of fawns fed concentrate diets was 15% higher than that of fawns fed browse diets and up to 48% higher than that of fasted fawns. Elevated FMRs may also have been related to the behavioral stress that subordinate fawns endure at feeding sites (Ozoga 1972; Schwartzkopf 1990) or may simply reflect the variance inherent within the population. Additionally, the high isotope-flux rates measured in fawn M4 indirectly suggest that the high FMRs (FMR:BMR > 2.0) were valid because dosage rates were based upon the assumption that FMR:BMR ratios would be <2.0.

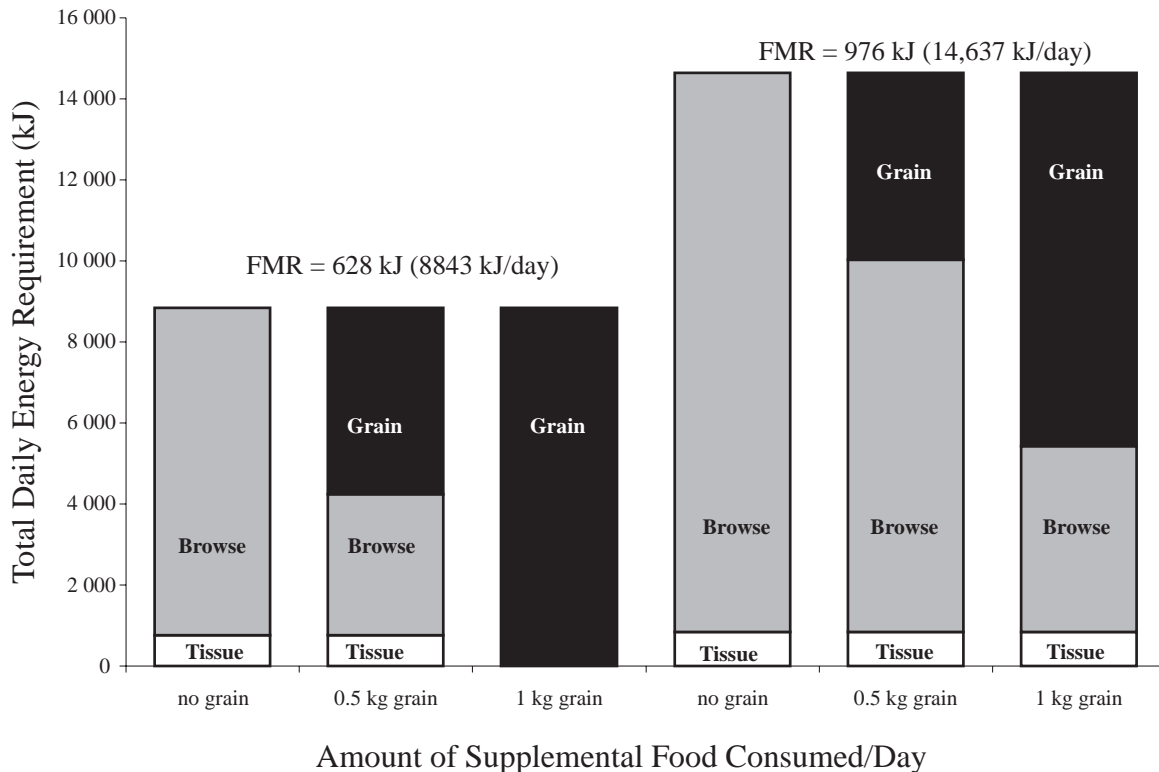
Although certain fawns were always precluded from eating by aggressive adults, it was clear that some consumed more grain than others and made behavioral changes that increased their access to supplemental food. We observed certain fawns moving between and feeding efficiently at grain piles to avoid dominant adults, and some bedded proximate to feeding areas to access grain quickly.

Although the mean FMRs of males and females were not statistically different, the mean FMR of male fawns was >30% higher. Assuming that fawn M4 also had a high FMR, given its isotopic concentrations, three of four males had FMR:BMR ratios >2.0. Conversely, only one of five females had an FMR above the median (690). Because male fawns weigh more than female fawns, but have higher absolute food requirements and similar body-fat reserves (Table 2), they may be more susceptible to winter mortality (Taber and Dasmann 1954).

It is possible to model the influence or substitutive effect of supplemental feed on measured FMRs, percent body fat and associated tissue energy, and browse-consumption rates. Additionally, manipulating the amount of grain consumed by fawns provides insight into the different foraging strategies that may have allowed certain fawns (M2, M3, F5) to operate at elevated FMR ($>2 \times$ BMR). Considering first fawns with FMR:BMR ratios <2.0, the average FMR of these individuals was $628 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ (Table 4), average body mass was 34 kg, and average percent body fat was 11% (Table 4). We assumed that winter lasted 90 days, at the end of which fawns had lost all fat (3.7 kg). We modeled three separate scenarios of the availability of daily grain: 0, 0.5, and 1.0 kg. Grain was worth $9211 \text{ kJ}\cdot\text{kg}^{-1}$, based upon the nutritional value of UNH deer feed (Worden and Pekins 1995). The caloric value of mass loss was estimated from the equations of Robbins (1993).

Over a 90-day winter period, the total energy requirement for fawns with an FMR of $628 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ was 795 827 kJ or 8 842 kJ/d (Fig. 1). When fawns consumed 0.5 kg grain/d, grain provided 414 493 kJ or 4 605.5 kJ/d. Grain and tissue energy represented 52.0 and 8.6% of the daily energy requirement, respectively, leaving 3475 kJ (39.4%) required from browse to satisfy FMR (Fig. 1). That proportion is equivalent to about $247 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ or about 845 g of typical winter browse (assuming 7.5 kJ metabolizable energy $\cdot\text{g}^{-1}$,

Fig. 1. Estimated contribution of tissue energy, browse, and supplemental food (grain) to the daily energy requirement of white-tailed deer (*Odocoileus virginianus*) fawns during a hypothetical 90-day winter in northern New Hampshire. Fawns with a FMR of $628 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ($8\,843 \text{ kJ/d}$) had a mean body mass of 34 kg; fawns with a FMR of $976 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ ($14\,637 \text{ kJ/d}$) had a mean body mass of 37 kg. We assumed that all fawns had 11% body fat that was depleted at 90 days. Fawns given 0.5 kg of grain would have difficulty consuming sufficient browse to achieve energy balance at $\text{FMR} = 976 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$.



80% metabolizable energy coefficient (Robbins 1993), applied to 9.4 kJ digestible energy/g (Gray and Servello 1995). This consumption rate is attainable on typical winter browse, as the digestible energy intake (DEI) of captive fawns consuming winter browse exceeded this level (Gray and Servello 1995), and the estimated MEI of a free-ranging fawn during winter in New Hampshire was $439.6 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ (Pekins 1995; P.J. Pekins, unpublished data). However, when fawns consumed 1.0 kg grain/d, providing 828 986 kJ or 9 211 kJ/d, they realized 104% of their daily energy requirement from grain alone.

Fawns with $\text{FMR} > 2 \times \text{BMR}$ had a mean FMR of $976 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$, an average body mass of 37 kg, and 11% body fat. Over a 90-day winter period, their energy requirement was 1 317 335 kJ or 14 637 kJ/d (Fig. 1). If they consumed 0.5 kg grain/d, grain and tissue energy represented 31.0 and 5.8% of the daily energy requirement, respectively, leaving 9186 kJ (63.2%) required from browse to satisfy FMR (Fig. 1). That proportion is equivalent to $611 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ or about 2.2 kg browse, an amount exceeding the DEI of captive fawns consuming high-energy browse diets (Gray and Servello 1995). When fawns consumed 1.0 kg grain/d, grain and tissue energy provided 63.0 and 5.8% of the daily requirement, respectively, leaving 4580 kJ (31.2%) or about $306 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ required from browse to satisfy FMR (Fig. 1). This energy can be obtained through consumption of winter browse (Gray and Servello 1995; Pekins 1995).

The influence of supplemental feed on the energy expenditure of fawns becomes evident when grain is removed from the

habitat and fawns must eat browse as their only source of MEI. When no grain is consumed, fawns with a FMR of $628 \text{ kJ}\cdot\text{kg}^{-0.75}\cdot\text{d}^{-1}$ must consume 8081 kJ or about $578 \text{ kJ}\cdot\text{kg}^{-0.75}$ of browse (about 2.0 kg) daily, assuming catabolism of body fat (Fig. 1). This level of browse consumption was beyond intake rates measured by Gray and Servello (1995), indicating inevitable mass loss and the improbability of fawns maintaining a high FMR continuously without supplemental feed. The high FMRs were probably reflective of constant availability and use of grain because body mass and body-fat content of most fawns were similar.

Browse consumption by fawns is influenced by browse availability, home range, and snow depth. Typical overbrowsing of habitat proximate to feed sites (Ozoga and Verme 1982; Schmitz 1990) may compromise consumption of sufficient browse to balance energy needs. There were more feeding sites and less natural browse at River Road than at Route 3, yet River Road fawns had smaller home ranges and higher percent body fat than Route 3 fawns. Fawns at River Road probably had greater access to supplemental feed than fawns at Route 3, and their relative nutritional status was not impacted by browse availability. It is possible that fawns at Route 3 had larger home ranges because supplemental food was less available and their consumption of browse was necessarily greater; predicted percent grain in the diet was generally higher at River Road sites than at Route 3 sites (Table 1).

The potential influence of supplemental feeding on the energy balance of deer is primarily dependent upon the interaction of deer density and food availability relative to

winter severity. Furthermore, deer density at feeding sites generally increases throughout winter, as well as annually (Sage and Gustafson 1988). Thus, the associated increase in nutritional requirements of a larger, local deer population may reduce the relative influence of supplemental feeding, particularly if the cost of pelleted grain limits food availability. The moderate winter severity during this study probably prevented the occurrence of severe malnutrition; however, the differences measured at River Road and Route 3 point to the probability that the nutritional influence of supplemental feeding is probably site-specific. The data did not indicate that supplemental feeding increased the nutritional status of all fawns, and most lost mass in the study. Adaptive behavior by certain fawns may increase their access to supplemental food, provide for increased daily MEI and reduced endogenous tissue catabolism, and ultimately increase their nutritional status during winter. However, certain fawns, or perhaps any deer, may be excluded from supplemental feed by dominant deer. Because adult deer have proportionally greater fat reserves and lower energy requirements than fawns, supplemental feeding should have less influence on their nutritional status during winter. The data indicate that biologists should expect variable nutritional status at typical supplemental feeding sites depending upon local deer density, sex and age ratios, feeding practices, and winter severity.

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