

Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer

Katherine L. Parker, Michael P. Gillingham, Thomas A. Hanley, and Charles T. Robbins

Abstract: Foraging efficiency (metabolizable energy intake/energy expenditure when foraging) was determined over a 2-year period in nine free-ranging Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska, and related to foraging-bout duration, distances travelled, and average speeds of travel. We calculated the energy-intake component from seasonal dry matter and energy content, dry matter digestibility, and a metabolizable energy coefficient for each plant species ingested. We estimated energy expenditures when foraging as the sum of energy costs of standing, horizontal and vertical locomotion, sinking depths in snow, and supplementary expenditures associated with temperatures outside thermoneutrality. Energy intake per minute averaged 4.0 times more in summer than winter; energy expenditure was 1.2 times greater in summer. Animals obtained higher amounts of metabolizable energy with higher amounts of energy invested. Energy intake during foraging bouts in summer was 2.5 times the energy invested; in contrast, energy intake during winter was only 0.7 times the energy expended. Changes in body mass of deer throughout the year increased asymptotically with foraging efficiency, driven primarily by the rate of metabolizable energy intake. Within a season, summer intake rates and winter rates of energy expenditure had the greatest effects on the relation between foraging efficiency and mass status. Seasonal changes in foraging efficiency result in seasonal cycles in body mass and condition in black-tailed deer. Body reserves accumulated during summer, however, are essential for over-winter survival of north-temperate ungulates because energy demands cannot be met by foraging alone.

Résumé : L'efficacité de la quête de nourriture (absorption d'énergie métabolisable / dépense énergétique au cours de la quête) a été déterminée au cours d'une période de 2 ans chez neuf Cerfs-mulets de Sitka (*Odocoileus hemionus sitkensis*) en liberté, en Alaska; la relation entre cette mesure et la durée des périodes de quête de nourriture, la distance parcourue et la vitesse moyenne des déplacements a été examinée. Nous avons évalué l'absorption de l'énergie en mesurant chaque saison le contenu en matières sèches et le contenu énergétique, la digestibilité des matières sèches et le coefficient d'énergie métabolisable par chaque espèce de plante ingérée. Nous avons estimé la dépense énergétique au cours de la quête de nourriture en faisant la somme des coûts énergétiques reliés à la station debout, aux déplacements horizontaux et verticaux, à la profondeur de l'enfoncement dans la neige, et des coûts additionnels associés aux températures situées hors de la zone thermoneutre. L'absorption d'énergie par minute était en moyenne 4,0 fois plus élevée en été qu'en hiver et la dépense énergétique était 1,2 fois plus élevée en été. Les animaux absorbaient plus d'énergie métabolisable lorsqu'ils investissaient plus d'énergie. La quantité d'énergie absorbée au cours des périodes de quête de nourriture en été était 2,5 fois la quantité d'énergie investie; en revanche, la quantité d'énergie absorbée en hiver équivalait à seulement 0,7 fois l'énergie dépensée. Les changements de masse des cerfs durant toute l'année augmentent selon une fonction asymptotique avec l'efficacité de la quête de nourriture, surtout à cause du taux d'absorption d'énergie métabolisable. Au cours d'une saison, c'est le taux d'absorption d'énergie au cours de l'été et la dépense énergétique au cours d'hiver qui constitue le facteur déterminant de la relation entre l'efficacité de la quête de nourriture et le statut relié à la masse. Les changements saisonniers dans l'efficacité de la quête de nourriture sont responsables des cycles saisonniers de la masse corporelle et de la condition physique chez le Cerf-mulet. Les réserves accumulées au cours de l'été sont cependant essentielles à la survie au cours de l'hiver chez les ongulés de la zone tempérée nord, car leurs besoins énergétiques ne peuvent être comblés par la seule quête de nourriture.

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Introduction

Recent advances in the ecology of wild ungulates have furthered our understanding of diet selection and feeding behaviour from a functional or mechanistic standpoint. Foraging efficiency (rate of energy or nutrient intake in relation to energy expenditure) is central to that understanding. It is assumed to have direct relevance to animals in both ecological and evolutionary contexts and has been the focus of study and modelling in a variety of organisms (reviewed by Stephens and Krebs 1986). Defining the currency that best characterizes the costs and benefits of animal foraging, however, continues to challenge researchers. Further, the temporal scale over which the costs and benefits should be measured may vary with the organism (e.g., Gass and Roberts 1992). Nonetheless, simulation models have attempted to describe the consequences of net resource intake in terms of spatial movements and landscape ecology (e.g., Roese et al. 1991; Turner et al. 1993). In the case of ungulates, foraging efficiency is very difficult to measure, especially for free-ranging, wild species in natural environments.

The foraging efficiency of an animal provides a critical link between food resources and body condition and performance. It is calculated from estimates of metabolizable energy intake divided by estimates of energy expenditure while foraging. Foraging efficiency has both physiological and ecological implications for an animal's survival. From an energy-intake perspective, animal needs are defined by physiological demands and influenced by nutritional status (Westoby 1974; Bunnell and Gillingham 1985). They are constrained by environmental parameters such as plant biomass and form, bite size, spatial distribution, and availability and quality of the forage (Illius and Gordon 1987; Gillingham and Bunnell 1989a; Laca and Demment 1992; Shipley and Spalinger 1992; Spalinger and Hobbs 1992; Gross et al. 1993). Nutrient intake is also affected by experience and learning (Gillingham and Bunnell 1989b) and the trade-off with inhibitory secondary plant compounds (Robbins et al. 1987). Similarly, energy expenditures reflect physiological requirements such as growth, reproduction, and lactation (e.g., Trudell and White 1981) and they are enhanced by seasonally variable environments that may affect locomotory and thermoregulatory costs. Therefore, physiological and ecological limits may affect either component of foraging efficiency in numerous ways. Further, the benefits of metabolizable energy intake to the animal are only relative to its expenditures. Foraging efficiency, in combination with summer-accumulated body reserves, determines the over-winter energy balance of many north-temperate ungulates.

In previous studies, foraging efficiency of ungulates has been assessed in indirect or incomplete ways, most often in terms of intake: e.g., feeding time achieved per unit distance travelled and the proportion of foraging time devoted to feeding (Owen-Smith 1979; Owen-Smith and Cooper 1983); the ability of the incisor breadth to enclose sufficient energy for the maintenance of body mass (Illius and Gordon 1990); dry-matter intake rate (Roese et al. 1991); and rates of digestible protein and energy intake (Langvatn and Hanley 1993). Such measures of intake efficiency further our understanding of food selection by the individual animal and have implications for the landscape distribution of populations (Gordon 1989a,

1989b) but do not necessarily relate to mass status or body condition. Other research has emphasized energy expenditures for specific activities in view of how energy constraints may control the foraging strategies of ungulates (see compilation by Fancy and White 1985); studies have concentrated on the energetic consequences of snow (Parker et al. 1984; Daily and Hobbs 1989) and extreme environmental temperatures (Parker 1988; Parker and Gillingham 1990), as they may influence activity patterns. We know of no studies, however, that have involved the simultaneous estimates of energy intake and expenditure by free-ranging ungulates in a natural environment year-round.

We monitored the energetics of foraging efficiency by tame, free-ranging Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) living year-round in a natural forest environment of southeastern Alaska, U.S.A. We calculated the simultaneous rates of energy intake and expenditure after making empirical measurements while following the animals. We analyzed the seasonal differences in these rates relative to one another and to biweekly changes in body mass during a 2-year period. The primary objective of the study was to further our knowledge of the concept of foraging efficiency as a critical link between food resources and body condition and performance. In addition, we hypothesized that (i) foraging efficiency would be driven primarily by metabolizable energy intake, as suggested by simulation models (e.g., Hobbs 1989); (ii) foraging efficiency would differ between summer and winter because the rates of energy intake and expenditure differ seasonally; and (iii) changes in body mass would be directly related to foraging efficiency. We also examined relations between the foraging efficiency of black-tailed deer and the duration of foraging bouts, distances travelled, and average speeds of travel.

Materials and methods

Subject animals

Nine Sitka black-tailed deer were hand-reared (2 males and 2 females born in 1987; 2 males and 3 females born in 1988) and weaned onto the natural vegetation of a 65-ha island located 20 km southeast of Wrangell, Alaska (Channel Island, 56°22'N, 132°10'W; see Parker et al. 1993b). It was entirely forested, with a western hemlock (*Tsuga heterophylla*) – Sitka spruce (*Picea sitchensis*) overstory; understory vegetation was dominated by blueberry (*Vaccinium ovalifolium* and *V. alaskensis*), skunk-cabbage (*Lysichiton americanum*), and devil's-club (*Oplopanax horridum*). Mean monthly maximum and minimum temperatures on Channel Island were lowest during February in both years of our study (−1.9 and −3.9°C in 1989; −0.6 and −2.1°C in 1990); they were highest in July–August (15.8 and 14.4°C in 1989; 15.9 and 14.3°C in 1990). The greatest monthly snow depths, exceeding 80 cm, occurred during late January through early February 1990.

The deer were free-ranging and had access to any forage and water they encountered in the natural environment. They wore tip-switch-equipped radio collars (Model MOD-500, Telonics, Arizona, U.S.A.) so that activity could be monitored at one of two receiving stations located approximately 2 km by water from the island. Each receiving system consisted of a TR-2 receiver, TPD-2 processor, omnidirectional antenna (Model RA-6B; Telonics, Arizona), and timer-equipped Rustrak dual-channel strip-chart recorder (Series 300, Gulton Industries, New Hampshire, U.S.A.; Gillingham and Parker 1992). The deer also could be located readily on the island with radiotelemetry. They allowed observers

to be very close (0.5–1.0 m) for visual observations because they were hand-raised. We weighed all animals 2–4 times per month. Young (small) animals were weighed in box scales that they had been trained to enter as fawns and that could be hoisted by pulley off the ground. Older (larger) animals were weighed on a 1.2 × 1.2 m aluminum platform scale installed permanently on the island (Model 23-2520A, Fairbanks Scales, Vermont, U.S.A., with Ohaus Model I-20W indicator).

Foraging efficiency

Individual animals were randomly selected for observation throughout the 2-year study. Two observers worked with the same animal simultaneously to estimate energy intake and expenditure while following the animals during foraging bouts. Foraging bouts were defined as continuous intervals of food intake within active periods. They ended when 2 min had elapsed with no food intake or whenever playing or running behaviours occurred. Observations were made between October 1988 and September 1990 on animals older than 1 year. Observation periods ranged from 30 to 512 min, with >90% of the observations lasting more than 170 min.

Energy expenditure

One observer measured the distance travelled with a hipchain (Forestry Suppliers, Mississippi, U.S.A.) and the slopes of all inclines with a clinometer to calculate the appropriate energy costs of uphill and downhill movement. Net energy expenditures for horizontal and vertical locomotion were calculated from these measured distances and slopes using values determined for mule deer (*Odocoileus hemionus hemionus*; Parker et al. 1984). Net energy costs (Y ; $\text{kJ} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$) for horizontal movement were calculated as $Y = 0.0124\text{kg}^{-0.34}$, for upslope travel as $Y = 0.0251$, and for downslope movement as $Y = -0.0071$. When the deer were travelling in snow, increments to the cost of movement were calculated from the sinking depth of the animal. We used the equation developed for mule deer moving in dense snow: $Y = 1.23X^{0.223X}$, where Y is the relative increase in the net cost of locomotion as a percentage above the cost of travel without snow and X is the sinking depth of the animal as a percentage of its brisket height (Parker et al. 1984). Metabolic rates for standing by black-tailed deer were assumed to be $0.4071 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$ during winter and $0.4372 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$ in summer (Parker 1988).

The same observer also measured the thermal environment at deer height at the beginning and end of an observational period using a fast-responding thermocouple inside a black copper float to obtain black-globe temperature. Black-globe temperature is a thermal index that combines air temperature, wind, and solar radiation into an effective temperature that is more representative of what the animal is experiencing than air temperature alone (see Renecker and Hudson 1986). Documented thermoneutral zones for black-tailed deer are between -6 and 18°C during winter and 12 and 27°C during summer (Parker 1988). When black-globe temperatures were below the lower critical temperature during winter in our study, we estimated supplementary energy expenditures from the slope of increasing metabolic rate as a function of temperature. Standing metabolic rate below -6°C (Y ; $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$) in winter was calculated from the equation $Y = -0.00983X + 0.367$, where X is given in degrees Celsius (Parker 1988). Total energy expenditure by an animal during a foraging bout was estimated as the sum of all of the above expenditures.

Energy intake

The second observer recorded behavioural and forage intake data on a small waterproof portable computer with an internal clock (Husky Hunter, Northwest Signal Supply, Oregon, U.S.A.). Recorded behaviours were "standing, lying, walking, running, playing, feeding, drinking, grooming, nursing, cud chewing, uri-

nating, and defecating," each entered as a letter code. The duration of each type of behaviour could be calculated by a program that we adapted for this study because the time of entry was automatically recorded. Feeding was entered by numerical code for each plant species eaten, followed by the amount of that species eaten. The amount eaten was estimated from the number of "plant units" eaten, a plant unit being a species-specific size unit highly correlated with actual plant mass (Parker et al. 1993a). We routinely measured the wet and oven-dry (55°C) masses of all plant units.

Samples of the plant species and parts eaten by deer were collected 4–5 times per year for laboratory analyses at the University of Alaska Agricultural and Forestry Experiment Station, Palmer. Leaves of shrubs were analyzed separately from stems. Samples were oven-dried at 40°C on the island and stored in sealed plastic bags at room temperature until final drying to a standard 55°C for analysis. Samples were analyzed for total nitrogen with the Kjeldahl procedure, for gross energy with bomb calorimetry, and for neutral detergent fibre, acid detergent fibre, cellulose, lignin, and ash with sequential detergent analysis (Goering and Van Soest 1970) without sodium sulfite and as modified by Mould and Robbins (1982). All results were expressed on a 100°C dry mass basis.

We calculated digestible protein and dry matter on the basis of fibre composition with equations from Hanley et al. (1992). Biogenic silica content was assumed to be zero. Preliminary analyses using bovine serum albumin precipitation (BSA; Hagerman and Butler 1978) indicated near-zero protein-precipitating capacities of tannins in the forages ingested by black-tailed deer on Channel Island (C.T. Robbins, unpublished data), a phenomenon consistent with the results of other studies of shade-grown understory species in the forests of southeastern Alaska (Hanley et al. 1984; Van Horne et al. 1988; Rose 1990). Therefore, we assumed a BSA precipitation capacity of zero in the equations for all species except western hemlock. That species composed a substantial portion of the winter diet and had an average BSA-precipitating capacity of $0.139 \text{ mg BSA/mg forage dry matter}$ (C.T. Robbins, unpublished data).

We used the following apparent metabolizable energy coefficients (Robbins 1993, p. 306): 81.8% for forbs, grasses, and sedges; 80.6% for shrubs and winter browse stems; and 76.4% for conifers. These values help to compensate for the effects of oils, terpenoids, phenols, and resins that analysis of tannin precipitating capacity does not incorporate towards the reduction of protein and dry-matter digestion.

Metabolizable energy intake by an animal during a foraging bout was determined as the product of species-specific dry-matter intake, gross energy concentration, dry-matter digestibility, and the metabolizable energy coefficient.

Foraging efficiency

We calculated foraging efficiency for each observed foraging bout by dividing the animal's metabolizable energy intake by its energy expenditure and multiplying by 100.

Statistical analyses

We analyzed the data in terms of two seasons: summer (April through September) and winter (October through March). These two periods coincide with major differences in plant phenology and deer metabolic activity. They also enabled us to analyze seasonal differences while maintaining relatively large sample sizes within each season.

We used an α level of 0.05 for statistical significance in all analyses. Relations of metabolizable energy intake and energy expenditure as functions of foraging-bout duration, distance travelled, and average speed of travel were tested as simple linear regressions (SAS:REG; SAS Institute Inc. 1987). Seasonal differences in the slopes of the regressions were examined with analysis of covariance (SAS:GLM). Analysis of variance (SAS:ANOVA) was used

to test for differences between seasonal means when regressions were not statistically significant within the seasons. The statistical significance of the correlation between speed and distance was tested with Pearson's product-moment correlation (SAS:CORR).

We analyzed the effects of foraging efficiency on biweekly changes in body mass as a nonlinear curve-fitting problem (SAS:NLIN). We report R^2 as the percentage of variation explained by using a Michaelis-Menton model: $Y = c + [aX/(b + X)]$. We also used forward stepwise multiple regression (SAS:REG) to examine the relative importance of the components of foraging efficiency (energy gain: kJ, kJ · min⁻¹; energy cost: kJ, kJ · min⁻¹, duration, distance, speed) on mass change. Both linear and nonlinear models required that all variables must be significant at the 0.150 level to be included and to stay in the model.

We treated all foraging bouts and biweekly mass changes as independent observations because the observations were widely distributed in time throughout the 2-year period of study and resulted from a random selection of study animals. Data collection for each foraging bout required intense effort, so samples were too small to stratify by 9 animals and two seasons.

Results

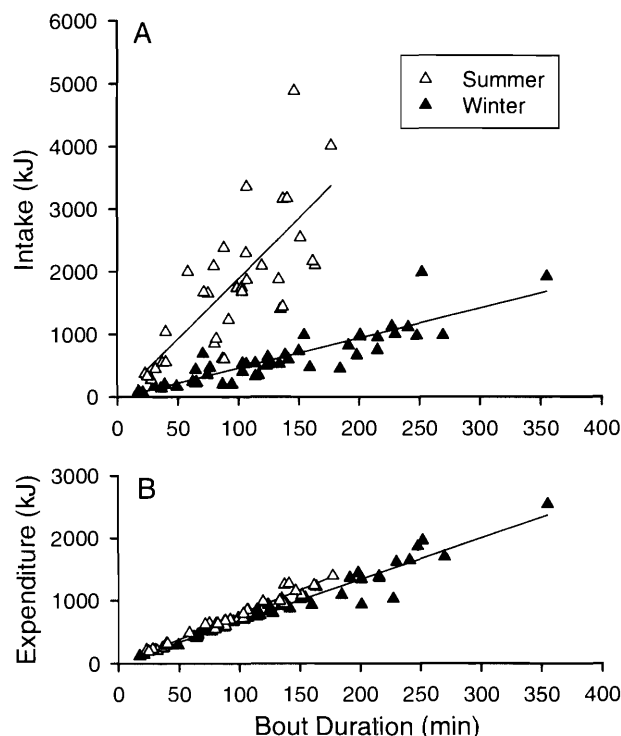
Rates of metabolizable energy intake by black-tailed deer did not differ among complete and incomplete bouts in summer or winter (all $P > 0.110$). Complete bouts were those during which the animal was observed continuously from the end of one lying period until it lay down again; incomplete bouts occurred when observations started or terminated during an active period. In our analyses, therefore, we combined the data from all foraging bouts, making a total of 78 separate bouts.

Major differences in foraging efficiency occurred between summer and winter. Intake rates of metabolizable energy within foraging bouts averaged 18.5 ± 7.0 kJ · min⁻¹ ($\bar{x} \pm$ SD) (0.40 ± 0.15 kJ · kg⁻¹ · min⁻¹; $n = 32$) during summer and only 4.6 ± 1.7 kJ · min⁻¹ (0.12 ± 0.04 kJ · kg⁻¹ · min⁻¹; $n = 46$) during winter. Rates of energy expenditure, on the other hand, averaged 7.8 ± 0.7 kJ · min⁻¹ (0.17 ± 0.02 kJ · kg⁻¹ · min⁻¹; $n = 32$) during summer and 6.8 ± 0.7 kJ · min⁻¹ (0.18 ± 0.01 kJ · kg⁻¹ · min⁻¹; $n = 46$) during winter. These rates were significantly different between seasons ($P < 0.001$). The seasonal differences in foraging efficiency that we calculated did not result from low temperatures or snow. Only 1 of the 78 measured bouts occurred when the environmental black-globe temperature was outside the thermoneutral zone (lower), and bouts on only 11 days involved elevated energy expenditures for locomotion in snow. Sinking depths in snow were <15 cm during all measured bouts.

Energy intake and expenditure

Both intake and expenditure of energy by black-tailed deer increased linearly with the duration of the foraging bout during summer and winter (Fig. 1; all $P < 0.001$). Rates of energy intake and expenditure in summer exceeded those in winter: the intake rate based on the slope of the regression was 4.0 times greater in summer than winter, whereas the expenditure rate was only 1.18 times greater. The principal environmental difference between summer and winter was the seasonal change in forage resources (e.g., typically 10 times the forage biomass and >1.5 times the average dry-matter digestibility in summer compared with winter in similar forests of southeastern Alaska; Hanley and McKendrick 1985).

Fig. 1. Metabolizable energy intake (A) and energy expenditure (B) of black-tailed deer in relation to duration of foraging bouts. In summer (April through September), energy intake (Y ; kJ) increased linearly as a function of bout length (X ; min) according to the equation $Y = 19.207X - 33.66$ ($n = 32$; $r^2 = 0.59$). This relationship differed significantly from that in winter (October through March, $P < 0.001$): $Y = 4.800X - 20.44$ ($n = 46$; $r^2 = 0.72$). Energy expenditure was also significantly different between summer ($Y = 7.832X + 5.29$, $r^2 = 0.97$) and winter ($Y = 6.652X + 8.95$, $r^2 = 0.94$) ($P = 0.015$).

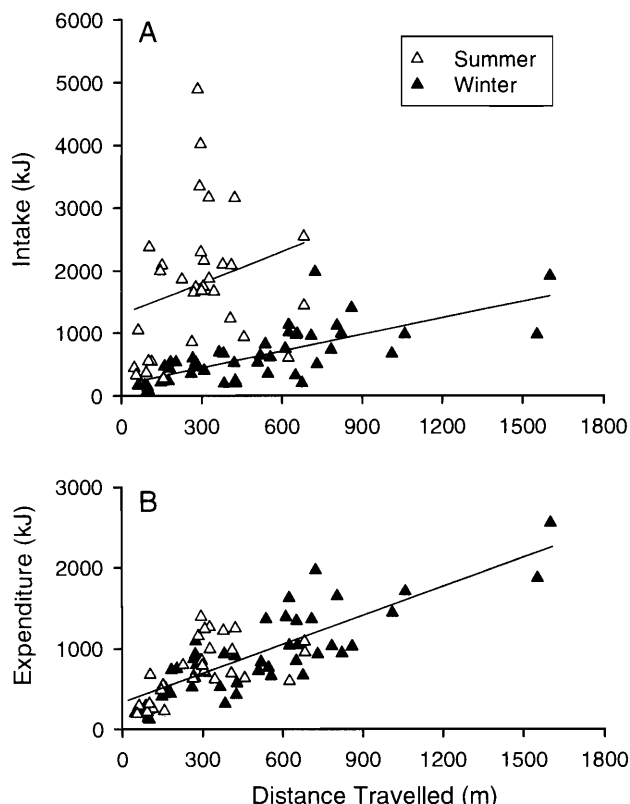


This change in food resources resulted in the seasonal difference in energy-intake rates (Fig. 1A).

The distance travelled by black-tailed deer was positively correlated with the average speed of travel ($r = 0.471$), with no significant seasonal differences ($P = 0.099$). Energy intake was not related to distance travelled during summer, but increased with distance in winter (Fig. 2A; $P < 0.001$). Energy expenditure increased with the distance travelled during both summer and winter (Fig. 2B; $P < 0.001$). The intake in winter was usually much less than in summer regardless of the distance over which the deer foraged. Even after travelling 3 times farther in winter (900 m), for example, the animals obtained only slightly more than a third (975 kJ) of the average energy ingested per bout during summer (2785 kJ; 275–325 m).

Relative to the average speed of travel (Fig. 3), animals obtained more metabolizable energy when travelling slower in summer ($P = 0.030$). Energy intake was independent of speed during winter. Energy expenditure was also independent of the speed of travel during both summer and winter ($P > 0.425$), probably because variations in speed were averaged over the entire bout. The energy costs of greater speed and uphill travel were generally offset by lower costs for slower movement and downhill locomotion.

Fig. 2. Metabolizable energy intake (A) and energy expenditure (B) of black-tailed deer in relation to distance travelled during a foraging bout in summer (April through September) and winter (October through March). Energy intake (Y ; kJ) varied significantly with distance travelled (X ; m) only in winter, according to the equation $Y = 0.885X + 178.45$ ($n = 46$; $r^2 = 0.51$, $P < 0.001$). Energy expenditure increased during both seasons as $Y = 1.191X + 340.39$ ($n = 78$; $r^2 = 0.62$), with no significant seasonal differences in slope ($P = 0.995$).



The major seasonal differences in foraging efficiency are most evident when the intake of metabolizable energy per foraging bout is plotted against the expenditure of energy (Fig. 4). Animals always obtained more metabolizable energy with the investment of more energy. Energy intake increased at a rate 2.54 times that of energy expenditure during summer, however, compared with 0.71 times during winter. Foraging efficiency in summer, therefore, was determined primarily by energy intake (because intake varied much more than expenditure). Foraging efficiency in winter, on the other hand, was more strongly determined by variation in energy expenditure than in intake.

Mass change

Biweekly changes in body mass varied as an asymptotic function of foraging efficiency (Fig. 5). At 100% efficiency, the calculated energy expenditure of the animal equals the metabolizable energy obtained from the food. That all animals did not gain mass at foraging efficiencies greater than 100% or lose mass at efficiencies less than 100% was probably due to the different time scales involved. Foraging efficiency was calculated per bout; mass change was measured per biweekly

Fig. 3. Metabolizable energy intake (A) and energy expenditure (B) of black-tailed deer in relation to the average speed of travel during a foraging bout in summer (April through September) and winter (October through March). Only the relation for energy intake (Y ; kJ) in summer was statistically significant: $Y = -308.160X + 2744.25$, where X is in metres per minute ($n = 32$; $r^2 = 0.15$; $P = 0.030$).

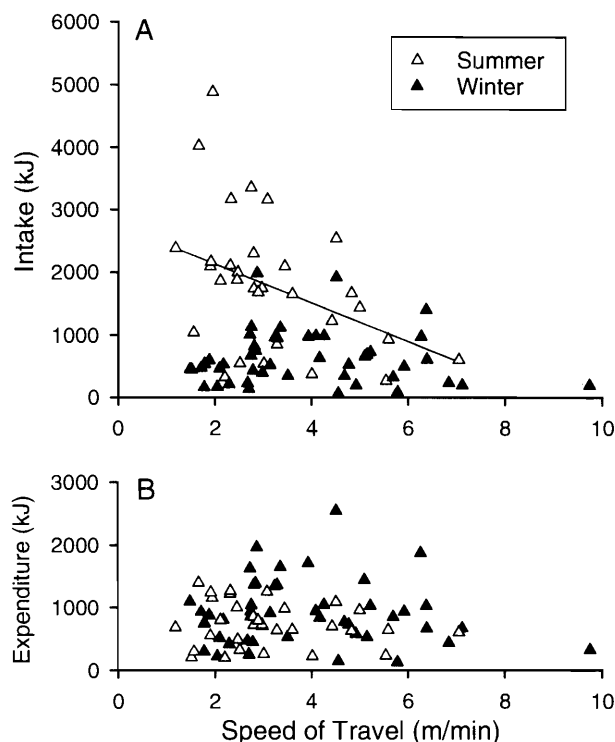


Fig. 4. Metabolizable energy intake of black-tailed deer in relation to energy expenditure during foraging bouts in summer (April through September) and winter (October through March). In summer, energy intake (Y ; kJ) increased linearly with energy expenditure (X ; kJ) according to the equation $Y = 2.541X - 85.86$ ($n = 32$; $r^2 = 0.66$). During winter, $Y = 0.713X - 18.98$ ($n = 46$; $r^2 = 0.74$). The slopes differed significantly from one another and from 1.0 ($P < 0.001$).

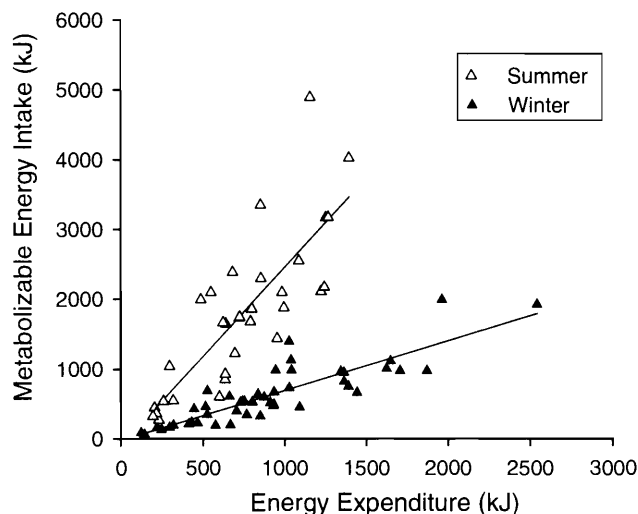
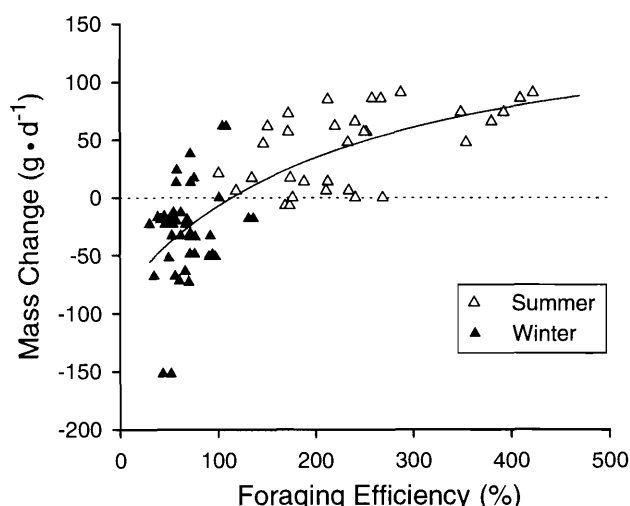


Fig. 5. Biweekly changes in mass of black-tailed deer in relation to foraging efficiency (metabolizable energy intake \div energy expenditure $\times 100$) determined during foraging bouts in summer (April through September) and winter (October through March). Mass change (Y ; g/d) increased asymptotically as a function of foraging efficiency (X) according to the equation $Y = [259.83X / (233.80 + X)] - 85.22$ ($n = 78$; $R^2 = 0.55$).



period closest to the bout. In fact, at maintenance levels, efficiency would be expected to be greater than 100% within foraging bouts to cover the additional demands of other activities such as resting that occur over the biweekly time scale. Foraging efficiencies were lowest in winter (less than one-fourth of those attained in midsummer) and associated with mass loss; they were highest in summer when animals were gaining mass. The relation is not a simple summer–winter dichotomy, however, but rather a graduated nonlinear function with foraging efficiency accounting for 55% of the variation in mass change.

The single most important factor determining foraging efficiency of the animal throughout the year was metabolizable energy intake per minute (partial $r^2 = 0.51$, $P < 0.001$). On a seasonal basis, stepwise multiple regression confirmed the conclusions based on the comparison of slopes and variation in Fig. 4. The rate of energy intake was most important in summer (partial $r^2 = 0.35$, $P < 0.001$). In winter, however, the rate of energy expenditure had the greatest effect on mass status (partial $r^2 = 0.15$, $P = 0.008$). The energy-intake rate was the second most important and only other variable included to significantly affect mass change in winter (partial $r^2 = 0.07$, $P = 0.06$; other variables tested included absolute energy intake and energy expenditure, duration, distance, and speed).

Discussion

Foraging efficiency

The foraging efficiency of black-tailed deer had measurable ecological and physiological consequences. It was most affected on a yearly basis by the intake rate of high quality forage. Significant within-season differences, however, were found. The rate of metabolizable energy intake dominated

during summer, whereas the rate of energy expenditure was most important in winter. The seasonal changes in rates of energy cost and gain between summer and winter resulted in major seasonal differences in foraging efficiency. Rates of energy intake varied much more than did expenditures. And foraging efficiency was directly related to changes in body mass.

Our results also indicate some more subtle aspects of foraging efficiency and reemphasize the critical importance of summer-accumulated body reserves for over-winter survival of north-temperate ungulates. The values that we determined for foraging bouts in winter are likely conservatively high estimates of average foraging efficiency because the deer often encountered greater snow depths and lower temperatures, especially at night, than those measured when the data were collected. It is also possible that although deer were seldom outside the thermoneutral zone reported for standing animals, activity levels may have reduced thermal insulative values and increased thermoregulatory expenditures. The deer obtained more energy the longer they foraged and the farther they travelled, but simultaneous energy expenditures also increased (Figs. 1 and 2). The greater slopes for energy expenditure than for intake indicate that there were no positive solution sets when the animals' energy intake equalled or exceeded expenditure during winter. In other words, foraging efficiency was less than 100% no matter how long the deer foraged or how far they travelled. The slope of energy intake as a function of expenditure (i.e., foraging efficiency), therefore, was less than 1.0 during winter (Fig. 4). The only times when energy intake exceeded expenditure during winter occurred at the extremes of our categorization of seasons, when high-quality forage was still available: in early November, when the animals were consuming large amounts of mushrooms, ferns (*Dryopteris dilatata*, *Blechnum spicant*), and the remaining centres of skunk-cabbage plants, and in late March, when they were foraging on the newly emerging leaves of skunk-cabbage and blueberry.

By contrast, energy intake during summer always exceeded energy expenditure regardless of bout duration, distance travelled, or speed of travel. For black-tailed deer in this ecosystem, energy intake equalled energy expenditure after only 2.5 min of foraging in summer. Greater foraging efficiencies were generally associated with greater mass gains (Fig. 5). The abundance of food resources in summer resulted in greater rates of energy intake, foraging efficiency, and mass gain than were ever possible during winter.

The importance of the availability of high-quality forage is reflected in numerous aspects of this study: black-tailed deer often travelled farther in search of food during winter (Fig. 2), they obtained more energy and showed highest rates of intake when travelling at slowest speeds during summer (Fig. 3A), and metabolizable energy intake rates were 4 times greater in summer than in winter (Fig. 1A). After expending the same amount of energy, forage energy gain was approximately 3.5 times higher in summer than in winter (Fig. 4).

Daily energy balance

If we assume that our observations of foraging behaviour were representative of activity throughout the day, then we can use our data from radiotelemetric recordings to deter-

mine the proportion of the day that each of our animals was active and multiply that time by its rate of energy intake ($\text{kJ} \cdot \text{min}^{-1}$) to estimate daily intake of metabolizable energy. We can estimate daily energy expenditures in a similar manner, assuming that the cost of standing is 25% greater than the cost of lying (inactivity) (Parker et al. 1984).

The daily proportion of time spent active by black-tailed deer during the 78 foraging efficiency trials was significantly greater during summer (53.0%) than during winter (49.0%; $P < 0.001$). Body mass of our animals ranged from 35 to 57 kg (46.2 ± 5.5 kg; $\bar{x} \pm \text{SD}$) during summer and from 34 to 47 kg (38.8 ± 3.3 kg) during winter. Although the deer were active for slightly less of the day and were assumed to have lower seasonal metabolic rates in winter than in summer, they also had greater costs of movement when travelling farther in search of food in winter than in summer. Estimated daily metabolism based on calculations for individual animals differed significantly, but only slightly, between seasons, averaging $573 \pm 29 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ in summer and $547 \pm 25 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ in winter. These values are similar to those theorized to be necessary for survival (1.9–2.0 times basal metabolic requirements; Moen 1985). Estimated daily metabolizable energy intake, on the other hand, was 3.8 times greater in summer ($798 \pm 318 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$) than in winter ($209 \pm 72 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$). Daily energy intake, therefore, was greater than 139% of daily expenditure in summer and less than 39% of energy expenditure in winter.

Such calculations should not be generalized to represent average seasonal daily energy metabolism of black-tailed deer because the costs of reproduction, including gestation and lactation, were not included in summer, and additional thermoregulatory and locomotory expenditures may have occurred during winter. The data illustrate, however, that forage resources are extremely important in controlling daily energy balance and, ultimately, mass status of black-tailed deer.

Foraging strategies

Recent models have examined the integration of two views of foraging: that focusing on food selection, which relates to energy intake, and that emphasizing activity under a given set of environmental conditions, which relates primarily to the rate of energy expenditure (see Goolish 1992). We estimated both energy intake and expenditure from simultaneous empirical measurements. Foraging efficiency was most affected by the rate of energy intake during summer. This result complements modelling efforts that have shown energy intake to be the most sensitive variable affecting energy balance in ungulates (Wickstrom et al. 1984; Fancy 1986; Hobbs 1989).

Variation in foraging efficiency of black-tailed deer during winter, however, was more strongly affected by variation in energy expenditure than by variation in intake (Fig. 4; stepwise multiple regression analysis). Murray (1991) noted that energy costs of locomotion could constitute a large fraction of the daily intake of metabolizable energy. Additionally, efficient search and movement algorithms in foraging models have been shown to be very sensitive parameters in predicting foraging patterns under the low-resource conditions of winter (Turner et al. 1993). When high-quality food

was abundant, as during summer in our study, the effects of locomotory costs were of minimal significance for our deer. In winter, when energy expenditure while foraging exceeded energy intake, variation in energy expenditure became relatively much more important than in summer. Factors affecting locomotory or thermoregulatory costs, therefore, were more important in winter than in summer. The poor forage resources of winter were ultimately responsible for the low foraging efficiency values, but it is important to recognize that our deer were unable to compensate for the decline in forage by finding high-quality, profitable patches, and factors affecting energy expenditure dominated the variation in foraging efficiency. In our estimates of activity costs, we used standing metabolic rates reported for black-tailed deer that encompass seasonal changes in metabolism and the effects of food intake, and we assumed that locomotory costs were a fixed increment in addition to standing metabolic rates. The energy costs of activity constituted only about half of the energy expended while foraging; the other half came from continual basal metabolic costs that are incurred whether or not the animal is foraging (assuming the interspecific mean of $70 \text{ kcal} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ or $293 \text{ kJ} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$). Other studies have also determined that maintenance is the largest component of energy requirements for ungulates (Adamczewski and Hudson 1993).

Our data and analyses do not indicate whether the feeding strategies of black-tailed deer are more or less selective when forage abundance is great (Weckerly and Kennedy 1992; Murden and Risenhoover 1993) or whether the deer sought to maximize their net intake of energy each day (energy maximization) or to satisfy their daily requirements in the least amount of time necessary (feeding-time minimization; sensu Schoener 1971; Schmitz 1991). It seems likely, however, that when foraging efficiency is determined primarily by variation in energy expenditure (winter), deer should be most selective of the environmental conditions under which they forage. They should always be highly selective of food, but the choice of when to feed becomes increasingly important in winter. Deep snows and low environmental temperatures should favour a feeding-time minimization strategy in which animals attempt to meet requirements in the shortest time possible and reduce activity demands by lying during longer nonforaging periods. Studies on north-temperate ungulates (reindeer and caribou, *Rangifer tarandus*) similarly concluded that the large proportion of time spent lying during winter was indicative of poor forage quality or availability (Roby 1980; Russell and Martell 1986). The inability to maintain body mass in winter, combined with the ability to gain mass in summer, on the other hand, should favour an energy-maximization strategy during summer. The high-quality food resources of summer would reduce the influence of time constraints and allow animals to maximize intake. Models for another generalist herbivore, the moose (*Alces alces*), have also predicted that diet selection maximizes net energy intake during summer (Belovsky 1978), although predominant equations within the model have been questioned relative to their biological foundations (Hobbs 1990).

The deer in our study lost up to 30% of their body mass with the mobilization of fat and protein reserves during winter (Parker et al. 1993b). Spring green-up became critical for late-winter survival. Fat stores measured in these and

other animals on Channel Island were 4–5 times greater at the end of summer than in early spring (Parker et al. 1993b). The accumulated body reserves from summer were essential for over-winter survival, since energy demands could not be met by foraging alone. Our analysis of foraging efficiency indicates why the seasonal cycles in body mass and condition occurred in black-tailed deer. Our data and analysis also illustrate the vital importance of foraging efficiency as a critical link between food resources and animal performance.

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