Energy and Protein Balance of Free-Ranging Black-Tailed Deer in a Natural Forest Environment

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

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by

KATHERINE L. PARKER, MICHAEL P. GILLINGHAM,
THOMAS A. HANLEY, AND CHARLES T. ROBBINS

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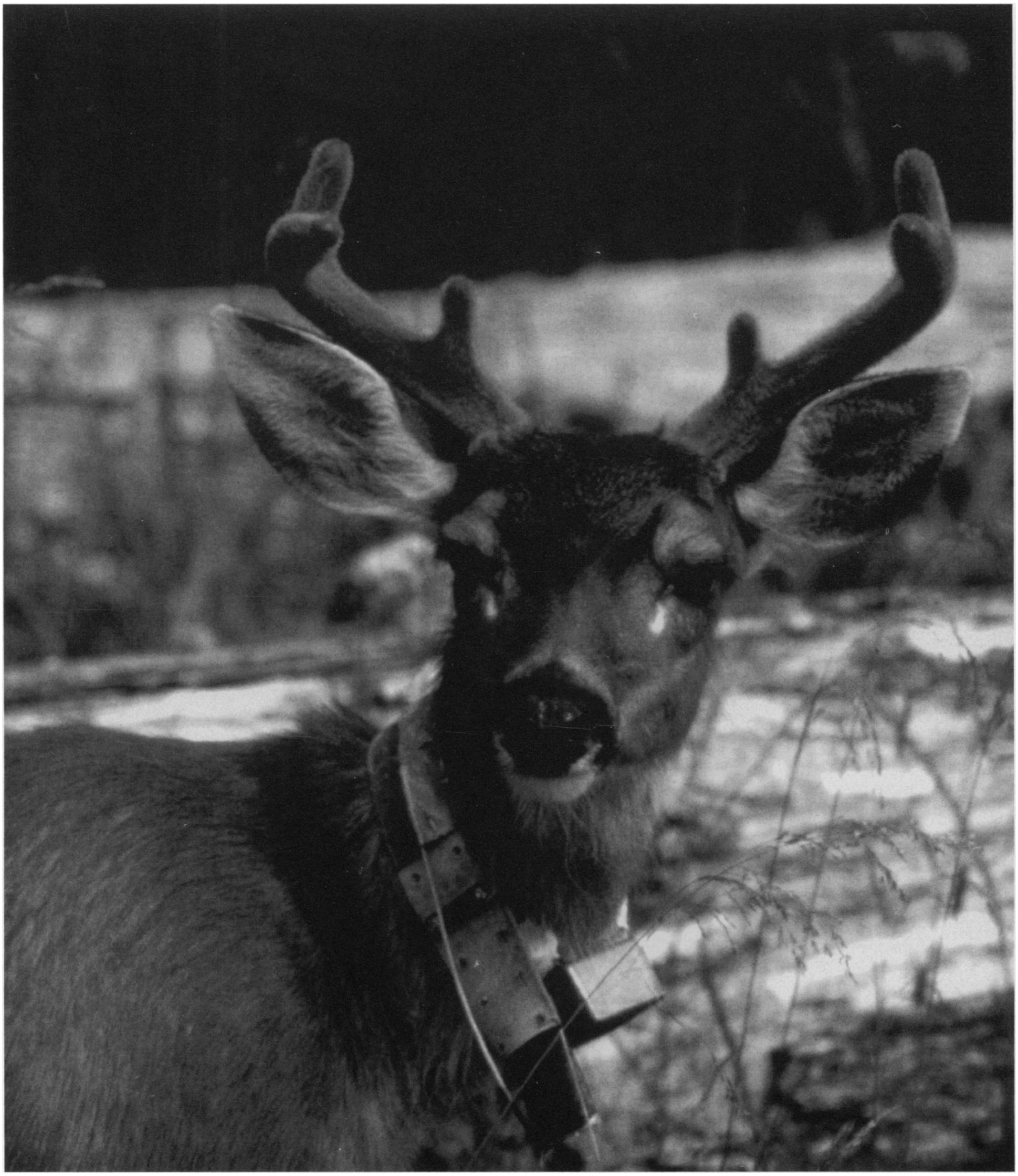

FRONTISPIECE. Sitka black-tailed deer on Channel Island, southeast Alaska (photo by Thomas A. Hanley).

ENERGY AND PROTEIN BALANCE OF FREE-RANGING BLACK-TAILED DEER IN A NATURAL FOREST ENVIRONMENT

KATHERINE L. PARKER

Faculty of Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada

MICHAEL P. GILLINGHAM

Faculty of Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada

THOMAS A. HANLEY

U.S.D.A. Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 2770 Sherwood Lane Suite 2A, Juneau, AK 99801-8545, USA

CHARLES T. ROBBINS

Departments of Natural Resource Sciences and Zoology, Washington State University, Pullman, WA 99164-6410, USA

Abstract: The purpose of this study was to quantitatively examine the validity of conclusions derived from reductionist studies of nutritional ecology of black-tailed deer. We measured protein and energy intake, activity budgets, and changes in body mass of free-ranging animals in a natural forest environment in relation to availability and nutritional quality of forage and environmental constraints (snow, temperature) over a 2-year period. We compared those observations of intake with modeled predictions of requirements. Daily protein intake remained above demands during all months of the year except February, whereas deer were unable to meet energy requirements for more than half the year. Compounded by increased demands associated with lactation during summer and with snow rather than temperature during winter, the availability of digestible energy is potentially the greatest nutritional limiting factor for black-tailed deer in Alaska. Changes in body mass were directly related to the ratio of energy intake to requirement. Body reserves accumulated during summer with abundant digestible energy were critical to winter survival. Reductionist studies of nutritional and physiological processes provided a strong mechanistic basis for understanding and predicting animal–habitat interactions in a natural environment.

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Key words: Alaska, black-tailed deer, deer, doubly-labeled water, energy balance, energy expenditure, energy intake, nutrition, *Odocoileus hemionus*, protein balance, protein intake.

CONTENTS

INTRODUCTION

Nutritional ecology is the science of relating an animal to its environment through nutritional interactions (Van Soest 1982, Robbins 1983). Energy and nutrient requirements, foraging and digestive efficiencies, and food abundances and qualities provide functional cause-and-effect relations that determine animal body condition, changes in body mass, and ultimately, reproduction and survival. Most such relations are physiological and quantitatively predictable. Nutritional ecology thus offers the prospect of a quantitative, predictive, and general theory of key relations between an animal species and its habitat. The implications for wildlife management and habitat evaluation are great (Moen 1973) and do not entail the ambiguities inherent in inferences from studies of habitat use or other behavior-based methods of habitat evaluation (Hobbs and Hanley 1990).

Deer of the genus *Odocoileus* are among the most studied of all wildlife in relation to nutritional ecology, with studies of practically all major physiological and nutritional linkages with their habitat. Because of its complex nature, however, nutritional ecology can be highly reductionist and compartmentalized. Individual processes are studied separately with the ultimate goal of linkage to understand animal–habitat processes. Despite the wealth of such studies for deer, syntheses of the components are rare and invariably have taken the form of computer simulation models (Moen 1973, Robbins 1973, Wickstrom et al. 1984, Hobbs 1989). Simulation models can be insightful, but any such insights rest on the validity of the underlying assumptions regarding key physiological processes and their linkages. The most valid synthetic conclusions would be drawn from a "synthesis" by the real animal in its natural environment.

Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) inhabit the coastal coniferous forests of southeast Alaska north of British Columbia, Canada, to Prince William Sound, Alaska. Their management has been politically controversial in recent decades because of their perceived dependence on old-growth forests for food and shelter and, therefore, direct conflict with clear-cut logging (Hanley 1993). Habitat-use studies have been most valuable in identifying important habitat variables (Wallmo and Schoen 1980, Schoen and Kirchhoff 1990, Yeo and Peek 1992), whereas nutritional ecology studies were most valuable in quantifying the importance of the variables and in identifying other, less apparent factors (Hanley et al. 1989). The habitat-use studies suffer from their site- and time-specific nature and lack of cause-and-effect mechanisms. The nutritional ecology studies provide a general theory of ecological processes, but suffer from their reductionist approach and lack of a whole-animal test of their integrated effects.

In this study we examine the validity of conclusions derived from the reductionist studies of nutritional ecology of black-tailed deer using live, free-ranging deer in a natural forest environment. Our chief interest was in the validity of ideas derived from the synthesis of reductionist components rather than the components themselves. We concentrated on a small group of deer in 1 case study rather than the general population of Sitka black-tailed deer across a variable range. Nonetheless, this is the first and only such intensive study of any wild ungulate species of which we are aware. Some specific details for black-tailed deer regarding seasonal changes in body weight and dynamics within foraging bouts only, rather than daily and seasonal strategies, were reported in Parker et al. (1993*a*, 1996) and Gillingham et al. (1997). Other studies also have contributed in less detail to our knowledge base (Belovsky and Jordan 1978, Owen-Smith and Cooper 1989, Renecker and Hudson 1989, Roese et al. 1991). In the present study, field observations different from our expectations would certainly be sufficient to cast doubt on the validity of earlier, general conclusions.

Theory and Predictions

Syntheses of the nutritional studies have been reported elsewhere (Wickstrom et al. 1984; Hanley et al. 1989, 1991; Hanley 1997). Those studies included forest environment (overstory–understory–snow relations) (Alaback 1982, 1984; Brady and Hanley 1984; Hanley and Rose 1987; Kirchhoff and Schoen 1987; Tappeiner and Alaback 1989; Alaback and Tappeiner 1991), forage availability and nutritional quality (Hanley and McKendrick 1983, 1985; Hanley 1987; Hanley et al. 1987; Van Horne et al. 1988; Rose 1990), dry matter and protein digestion (Robbins 1987; Robbins et al. 1987*a*,*b*, 1991; Hanley et al. 1992), rumen turnover and processing time (Spalinger et al. 1986, 1993; Spalinger and Robbins 1992), dry matter and energy intake rates (Wickstrom et al. 1984, Spalinger et al. 1988), diet selection (Hanley et al. 1985, Hanley and McKendrick 1985, McArthur et al. 1993), energy costs for locomotion and thermoregulation (Parker and Robbins 1984, Parker et al. 1984, Parker 1988, Parker and Gillingham 1990), and total energy balance (Wickstrom et al. 1984, Hanley and McKendrick 1985, Hanley and Rogers 1989, Hanley et al. 1991). The syntheses resulted in several conclusions that were expected to be relevant to Sitka black-tailed deer throughout most of their range. Our present study constituted a quantitative examination of the validity of those conclusions. Logistical constraints, however, limited our study area to one of a low-elevation forest environment without clear-cuts. Hence, our predictions were those involving black-tailed deer living year-round in a natural forest environment. Specifically, we expected the following, based on the above studies, strategies of other northern ungulates, and regional field observations:

1. Summer is critical for building body reserves even though greatest apparent nutritional stress occurs during winter. Typically, the nutritional requirements of winter cannot be met by foraging alone and depend to a large extent on catabolization of body stores (Mautz 1978, McCullough and Ullrey 1983). Those body reserves "buy time" for deer as a buffer against winter (Torbit et al. 1985). Therefore, foraging efficiency in summer has direct consequences for winter body condition and survival. Time budgets should be dominated by foraging throughout the year.
2. Intake of digestible energy is a greater nutritional limitation than is intake of digestible protein, on a year-round basis. Historically, this has been inferred because many northern ungulates starve during winter. The protein con-

tent of forage is much closer to meeting maintenance requirements of deer than is energy content, and rebounds rapidly during spring and summer (Wallmo et al. 1977).

3. Key forages for meeting energy and protein requirements vary seasonally. Based on plant chemical composition (Hanley and McKendrick 1983, 1985) (which provides insights into potential intake strategies), key forages in spring should include skunk cabbage (*Lysichiton americanum*), early greening forbs, and blueberry (*Vaccinium* spp.) leaves; in summer, forbs and shrub leaves; in fall, shrub leaves and late-growing forbs; and in winter, evergreen forbs (most important), arboreal lichens (for energy but not protein), blueberry twigs, and western hemlock (*Tsuga heterophylla*) seedlings (much lower quality than forbs and lichens). Dietary selection by deer corresponds accordingly.
4. During snow-free periods, blueberry twigs (although very abundant) contribute relatively little to daily digestible energy and protein intake. Following snows that are sufficient to bury the herb layer, diet is expected to shift from predominantly evergreen forbs to predominantly blueberry twigs. This shift causes the average diet to decrease significantly in both quantity (amount consumed per day) and quality (digestible energy and digestible protein), because of the added processing and passage constraints associated with less digestible (highly fibrous) browse species (Hanley 1982; Spalinger et al. 1986, 1988). Snows sufficient to bury herb-layer forbs, therefore, will have a large effect on the energy balance of deer, even if not deep enough to substantially increase costs of locomotion. If arboreal lichens (which contain high amounts of digestible energy) (Robbins 1987) are available, they may compensate for the loss of forbs and cushion the drop in the digestible energy content of the diet during periods of snow.
5. Winter dietary intake will never be sufficient to maintain positive energy balance. Consequently, body condition and mass will decrease throughout the winter to meet energy demands, with the rate of change being most strongly determined by dietary intake (influenced by snow, as above) rather than energy expenditure. Additional energy costs of locomotion in snow contribute a relatively small proportion of an animal's energy budget, whereas total energy intake may be markedly reduced by increased snow depths (Hobbs 1989).
6. Although energy costs associated with thermoregulation will be relatively minor on a year-round basis for deer in coastal environments, greatest effects on total energy budget are likely to occur for animals in summer pelage during cool periods of rain (Parker 1988).
7. Energy balance of deer year-round is most sensitive to variation in energy intake rather than energy expenditure (*see* 1 and 5 above; Fancy 1986, Hobbs 1989).

Together, these predictions describe a situation where availability and nutritional quality of forage (especially its digestible energy concentration) dominate all other environmental factors in determining the health, growth, and reproduction of individual deer. Forage resources are critical year-round, not just during the season of least availability. Certain forage classes (or species) are especially important, and their lack of availability may have serious consequences for deer. If such a picture is correct, then knowledge of forage resources in relation to animal metabolic requirements should provide a strong basis for prediction of habitat capability for populations of deer (i.e., an extension from the individual animal to the concept of "carrying capacity"; Hanley and Rogers 1989).

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METHODS

Study Area

Our study was conducted over a continuous 2-year period (Oct 1988–Sep 1990) on Channel Island, which is approximately 65 ha in size and located 20 km southeast of Wrangell, Alaska (56°22′N, 132°10′W). The island was entirely forested, dominated by a western hemlock overstory and a lesser component of Sitka spruce (*Picea sitchensis*) (*see* ecosystem description in Ruth and Harris 1979). Only minor amounts of selective logging occurred in the 1920's and 1930's on the island. Generally the forest was uneven-aged across the island, except for a small patch of even-aged blow-down in the southwest corner and a larger stand of older, even-aged blow-down on the northern end. Plant understory communities included 3 plant associations within the western hemlock series and a beach community, which allowed for a variety of habitat types offering food and cover. The forested associations were distinguished by the abundance in the understory of one of the following: (1) blueberry (*Vaccinium ovalifolium* and *V. alaskaense*), which was often found in combination with shield fern (*Dryopteris dilatata*, synonomous with *D. expansa*; Cody 1996), (2) skunk cabbage, or (3) devil's club (*Oplopanax horridus*) and blueberry (Pawuk and Kissinger 1989). Rusty menziesia (*Menziesia ferruginea*) and red huckleberry (*Vaccinium parvifolium*) also were present in small amounts in the tall blueberry shrub layer. The 3 associations are referred to hereafter as *Vaccinium* (to designate both blueberry and huckleberry), skunk cabbage, and devil's club habitats. As is typical of stable forested soils of the western hemlock series with thick organic duff layers, the forb layer was moderately productive and almost always included bunchberry dogwood (*Cornus canadensis*) and five-leaf bramble (*Rubus pedatus*). Both of those forbs remain green throughout the winter, and in combination with fern-leaf goldthread (*Coptis asplenifolia*) and trifoliate foamflower (*Tiarella trifoliata*), provide an important winter food resource for Sitka black-tailed deer. The 4 forbs are often referred to as evergreen or winter-green species because they remain green during winter, losing only some of their leaves, and growing new leaves in spring and summer. The beach community included sedges (*Carex* spp.), a variety of forbs, and beach fringe shrubs (*Alnus sinuata, Malus fusca*). General vegetation typing on Channel Island resulted in approximately 48% by area of *Vaccinium* communities, 32% devil's club understory, 17% skunk cabbage associations, and 3% beach fringe (Fig. 1; Pawuk and Kissinger 1989). Pockets of all habitat types, however, were

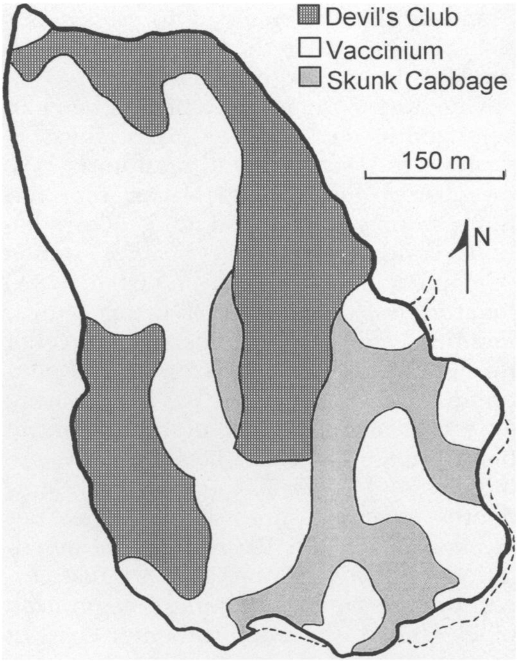

Fig. 1. Devil's club, *Vaccinium*, and skunk cabbage associations on Channel Island, southeast Alaska, as mapped by Pawuk and Kissinger (1989). Dashed lines indicate beach communities.

found within the mapped forest associations. Elevations on the island ranged from sea level to approximately 125 m.

Climate on Channel Island can be characterized as cool and wet, as is typical of southeast Alaska coastal rainforests. We monitored meteorological variables (air temperature, wind speed, and solar radiation) continuously at a weather station (Campbell Scientific, Logan, Utah, USA) located on the island. During winter months, which we defined as October through March, mean maximum and minimum air temperatures by month were lowest during February of both years of our study (−1.3 and −3.0 C°); they were highest in October (7.4 and 6.1 C°). Snow depths were measured at least once per week at 10 sites in 1989–90 and at an additional 14 sites during 1990–91 that corresponded with permanent vegetation plots. Unlike islands on the outer coast of southeast Alaska where snow depths can be minimal, the greatest monthly cumulative snow depths exceeded 80 cm in some areas on Channel Island during February 1990. During summer (Apr to Sep), mean maximum and minimum temperatures by month were lowest in April of both years (8.4 and 6.1 C°) and equally high in July and August (15.6 and 14.1 C°). The coldest air temperature recorded on Channel Island during the study was −17.1 C° in January 1989; the warmest temperature was 28.9 C° in July 1989.

Channel Island was selected for the study largely because of logistical constraints. A fenced area on the mainland large enough to conduct the project would have been economically prohibitive. The island site contained the study animals without the use of fencing and minimized potential problems with predation by bears (*Ursus americanus* and *U. arctos*) and wolves (*Canis lupus*) that existed on the mainland, although bears and other deer occasionally visited the island, but did not reside there. The size of the island was similar to the average home range size of nonmigratory black-tailed deer in Alaska (Schoen and Kirchhoff 1985) and, therefore, allowed each animal to be familiar with the whole island, yet not be constrained. The island supported a variety of forested habitats and received sufficient snow to accumulate a snowpack. The coastal environment facilitated access to the study site during winter and allowed for moorage of support facilities nearby. Also, the island was necessarily remote from major human centers.

Study Animals

We bottle-raised 9 Sitka black-tailed deer (2 males and 2 females born in 1987; 2 males and 3 females born in 1988) using a formula designed to simulate the nutrient profiles occurring naturally in deer milk (K. L. Parker, co-author, unpublished data; Parker et al. 1993*a*). The animals were weaned onto the natural vegetation of Channel Island and had access to any forage and water they encountered. They allowed observers to be very close (0.5–1.0 m) for visual observations because they were hand-raised. We weighed the deer 2–4 times per month, initially in box scales that they had been trained to enter as fawns and that could be hoisted by pulley off the ground. Subsequent measurements of mass were made on a 1.2 × 1.2-m aluminum platform scale installed on the island (Model 23-2520A; Fairbanks Scales, Saint Johnsbury, Vermont, USA, with Ohaus Model I-20W indicator). Data on body mass were collected opportunistically when deer were in the area of the scale.

Deer were equipped with tip-switch radiocollars (Model MOD-500; Telonics, Mesa, Arizona, USA) at 1 year of age and could be located readily using radiotelemetry. Daily activity was monitored at receiving stations approximately 2 km by water from the island. Each of 2 receiving systems consisted of a TR-2 receiver, TPD-2 processor, omnidirectional antenna (Model RA-6B; all from Telonics, Mesa, Arizona, USA), and Rustrak dual-channel strip-chart recorder (Series 300; Gulton Industries, Manchester, New Hampshire, USA). The data recording system was described in Gillingham and Parker (1992). We randomly chose 2 animals to be monitored telemetrically each 24-hr period over the course of the 2-year study. The continuous radio-telemetric records were sampled subsequently at 5-min intervals using a BASIC program we wrote to determine periods of activity and inactivity.

Reported data are from the 9 animals when they were older than 1 year of age. Of the 5 females, 2 (at 2 yr of age) produced single fawns during the first year of the study. In the second year, 2 singleton fawns and 2 sets of twins were born (i.e., only one 2-yr-old female did not reproduce).

Monitoring Activity and Forage Intake

We monitored behavioral and forage-intake data for individual deer over the continuous 2-year study period. Daily observations were recorded during a 2–8 hr period using a small waterproof computer (Husky Hunter; Northwest Signal Supply, Lake Oswego, Oregon, USA). Behaviors (standing, lying, walking, running, playing, drinking, grooming, nursing, cud-chewing, urinating, defecating) were entered by first letter codes. In addition, whenever an animal was feeding (ingesting food), the observer recorded a species-specific numerical code for the plant species eaten. The duration of each behavior was calculated from the difference in the time of each entry using a program that we adapted for the clock-equipped computer. Foraging behavior was defined in subsequent analyses as that time in which animals ingested and/or sought food as long as food intake did not cease for >2 min (Gillingham et al. 1997). Different plant parts ingested were recorded separately. The amount eaten also was recorded, based on "plant units" that were highly correlated with actual plant mass (Parker et al. 1993*b*). We measured the wet and oven-dry mass for all plant units every 2–3 months. Forage intake (g dry matter) during behavioral observations was then calculated from the number of plant units eaten of each species.

We estimated daily intake for black-tailed deer by multiplying an individual's intake rate (g/min) that we observed within an active period (time including all behaviors except standing in 1 place >5 min and lying) by the amount of time the animal was active (min/day), as determined by radio-telemetric recordings. A 2-week series of animal observations during nighttime hours in summer showed that nighttime foraging activities and species selection did not differ from those during daytime (K. L. Parker and M. P. Gillingham, co-authors, unpublished data). We therefore assumed that our observations of foraging behavior were representative of activity throughout the day.

Measures of Forage Quality

Samples of the plant species eaten by the deer were collected 4–5 times per year (chosen relative to phenological changes), oven-dried at 40 C°, and stored at room temperature. Leaves and stems were collected separately for *Vaccinium*, *Menziesia*, and *Alnus* shrubs, as were *Dryopteris* rhizomes and fronds. Laboratory analyses were conducted at the Agricultural and Forestry Experiment Station, Palmer, Alaska, USA. All samples were standardized to 55 C° dry mass before being analyzed for total nitrogen (Kjeldahl), gross energy (bomb calorimetry), and neutral detergent fiber, acid detergent fiber, cellulose, lignin, and ash (sequential detergent analysis without sodium sulfite; Goering and Van Soest [1970], as modified by Mould and Robbins [1982]). Results were expressed on a 100 C° dry-mass basis.

We calculated the apparent digestible protein and dry matter content of forages consumed by deer as in Hanley et al. (1992), using predictive equations from Robbins et al. (1987*a,b*). Biogenic silica content, which is usually associated with monocots and is a component of those equations, was assumed to be zero in our study. Another component, bovine serum albumin (BSA) precipitation, also was assumed to be zero for all species except western hemlock; BSA is used to determine the protein-precipitating capacity of forage tannins that reduce protein and dry matter digestion. Preliminary analyses showed that forages ingested by black-tailed deer on Channel Island had negligible tannin content except for western hemlock, which composed a large component of the winter diet and precipitated 0.139 mg BSA/mg forage dry matter (C. T. Robbins, co-author, unpublished data).

The net or useable protein intake by deer, which reflects how much absorbed nitrogen can be utilized for maintenance and production, was calculated from the product of the digestible protein intake and biological value. We used data for white-tailed deer (*Odocoileus virginianus*) to develop an equation for biological value (Y expressed in %) based on crude protein content of the diet (X expressed in %) selected during each foraging bout: $Y = 133.2766 \div (X^{0.32584})$ (Robbins 1983:304).

Metabolizable energy intake by deer, as a measure of energy that can be used for maintenance and production requirements, was determined from the product of digestible dry matter intake, gross energy content, and a metabolizable energy coefficient. Metabolizable energy coefficients help to compensate for the effects that oils, terpenoids, phenols, and resins have on dry matter digestion. We used apparent metabolizable energy coefficients of 81.8% for forbs, grasses, and sedges; 80.6% for shrubs and winter browse stems; and 76.4% for conifers (Robbins 1993:306).

General Trends in Forage Availability

Fourteen circular vegetation plots were established permanently on Channel Island to represent general trends in vegetative quality and quantity in the 3 common understory communities. Seven plots were located in areas dominated by *Vaccinium* understories, 4 plots in skunk-cabbage-dominated communities, and 3 plots in devil's club areas. Even though the communities were dominated by a particular understory species, individual plants of 1 or both of the other 2 understory communities also could be present. The 100-m^2 circular plots (5.64-m radius) were sampled 9 times during October 1989–August 1990.

A plot was divided into 8 equal-sized wedges (12.5 m^2) for ease of sampling. We assumed that shrubs always were available to the 9 deer on Channel Island and, given the time constraints associated with determining shrub biomass, we only estimated the percent cover of shrubs and conifers that were <2-m tall (within deer reach). In each wedge, we estimated ocularly the percent cover of *Vaccinium ovalifolium*, *V. alaskaense*, *V. parvifolium*, *Menziesia ferruginea*, *Rubus spectabilis*, *Sambucus callicarpa*, and *Tsuga heterophylla*. We also determined the biomass of "rare" items (newly emerging *Lysichiton americanum* centers, mushrooms, rhizomes, *Alectoria* and *Usnea* windblown from the treetops) and "large bite" items (*Lysichiton americanum* leaves, *Oplopanax horridus* leaves) using the system of plant units (Parker et al. 1993*b*). We used the lines defining each wedge as transects to sample the herb-layer forages (excluding any of the above items) in 5 0.1-m^2 rectangular quadrats placed at 1-m intervals starting from the outside edge of the plot. Within each quadrat, we recorded rooted biomass by species using the plant-unit technique. Vegetation quality (apparent digestible energy and protein) was determined as described above. Hence, we averaged measurements from 8 wedges and 40 quadrats in each 100-m^2 plot.

Calculation of Nutritional Requirements of Black-tailed Deer

Monthly protein and energy requirements were calculated with a simulation model for a fawn, an adult male, and an adult female black-tailed deer to show relative differences between sex and age. Calculated requirements for adults were compared with actual field observations of intake from the free-ranging animals on Channel Island. For the calculations, we used the average monthly body mass for fawns and adults (>15 months of age) (Parker et al. 1993*a*) (Fig. 2) and the av-

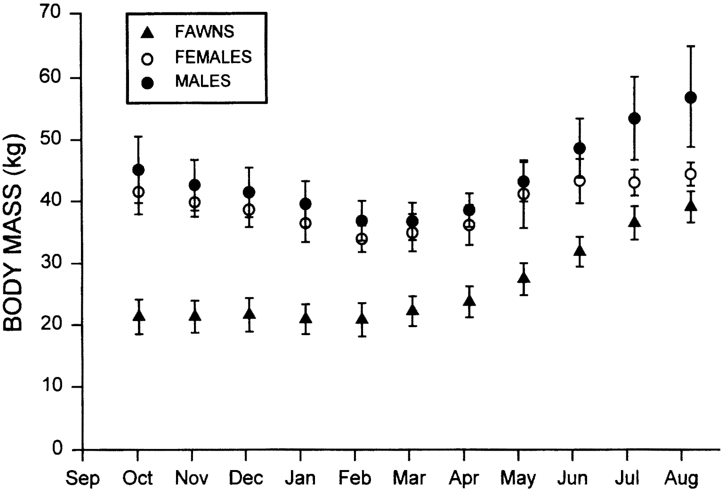

Fig. 2. Average monthly body mass of fawn and adult black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990. Average mass was used to model nutritional requirements.

erage amount of time spent active and inactive from radio-telemetric recordings.

Protein requirements for maintenance were calculated as the sum of endogenous urinary nitrogen and metabolic fecal nitrogen losses using values from Robbins et al. (1975). Endogenous urinary nitrogen was assumed to be similar to that in white-tailed deer (115 mg N$\cdot$kg$^{-0.75}\cdot$day^{-1}). Metabolic fecal nitrogen was estimated the same as for white-tailed deer and mule deer (*Odocoileus hemionus hemionus*): 7.81 g N/kg DM intake (where DM = dry matter and by assuming an average DM intake by month for fawns and for adult males and females; Gillingham et al. 1997).

The protein requirement for growth by black-tailed deer fawns and summer yearlings (g protein/g mass gain) was calculated as 0.20 kg$^{0.01}$ (Robbins 1973). Productive requirements for molting averaged 85% of endogenous urinary nitrogen losses (Robbins et al. 1974, Holleman and Dieterich 1978), and the requirement for antler growth was estimated to be 30% of endogenous urinary nitrogen (Robbins 1983: 225). Monthly nitrogen requirements for fetal growth (g N retention/kg fetus) were calculated as for white-tailed deer by $e^{0.0513X - 4.7014}$, where X is the stage of gestation from zero to 100% (Robbins and Moen 1975). We assumed a single fawn birth mass of 3 kg and twin birth mass of 6 kg and assumed a gestation period of 203 days (Anderson 1981:50). Protein demands (g N) for mammary gland development, which occurs primarily in the last third of gestation, were predicted from maternal body mass as 0.03 kg$^{0.79}$ (Robbins 1983:178). We calculated monthly protein demands for lactation using milk production (ml/day) and composition (g protein/ml) determined for a 45-kg black-tailed deer (Sadleir 1980). Protein requirements for nursing twin fawns were increased by a factor of 1.67 over that of single fawns (Robbins 1993:213).

Energy requirements of black-tailed deer were calculated assuming average expenditures during active periods of 0.435 kJ$\cdot$kg$^{-0.75}\cdot$min^{-1} in winter and 0.439 kJ$\cdot$kg$^{-0.75}\cdot$min^{-1} in summer, as determined from observations of individual foraging bouts (Parker et al. 1996). Those calculations were derived from seasonal metabolic rates for fed, standing adult black-tailed deer (0.4071 kJ$\cdot$kg$^{-0.75}\cdot$min^{-1} during winter and 0.4372 kJ$\cdot$kg$^{-0.75}\cdot$min^{-1} during summer) (Parker 1988), plus energy expenditures for horizontal and vertical locomotion by mule deer (Parker et al. 1984). Energy costs (above standing) per unit distance (Y expressed as kJ$\cdot$kg$^{-1}\cdot$m^{-1})

to move horizontally were calculated as $Y = 0.0124 \cdot \text{kg}^{-0.34}$, energy costs for upslope travel per vertical m increased above horizontal travel by $Y = 0.0251$, and energy costs for downslope travel per vertical m decreased by $Y = 0.0071$. Adjustments for the metabolic effects of increasing age in standing fawns were made using data from Parker (1988). Incremental increases in the cost of travel per unit distance during winter were added based on sinking depths in average monthly snow depths. We used the equation developed for mule deer moving in dense snow (which is typical in coastal environments): $Y = 1.23Xe^{0.223X}$, where Y is the relative increase in the cost of locomotion per unit distance 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). We determined the relationship for brisket height (Y expressed in cm) in relation to body mass (kg) of the black-tailed deer on Channel Island (by measuring standing animals to the nearest 0.5 cm on the platform scale) to be $Y = 13.28[\ln(X + 1)]^{0.9585}$ ($n = 17$, $r^2 = 0.92$; K. L. Parker, co-author, unpublished data). We also assumed that energy costs of foraging were 2% higher than those for standing, that expenditures for standing were 25% higher than lying, and that rumination increased lying costs by 2% (Fancy and White 1985).

We calculated additional energy expenditures associated with thermoregulation when environmental conditions exceeded limits of thermoneutrality for black-tailed deer (−6 to 18 C° during winter; 12 to 27 C° during summer; Parker 1988). The thermal index of operative temperature (T_e) was determined using biophysical models for each set of meteorological variables (air temperature, wind, and solar radiation) taken at the weather station on Channel Island and average animal characteristics for black-tailed deer (Parker and Gillingham 1990). The thermal index of operative temperature describes an effective temperature that is more representative of the environment experienced by an animal than is air temperature alone (Bakken 1992). When operative temperatures were below the critical thermal limits for black-tailed deer, we calculated supplementary energy expenditures for our animals from the slope of increasing metabolic rate as a function of decreasing temperature. Standing metabolic rate (Y expressed as $\text{kJ} \cdot \text{kg}^{-0.75} \cdot \text{min}^{-1}$) was calculated below −6 C° in winter from the equation $Y = -0.0098X + 0.367$ and below 12 C° in summer from $Y = -0.0129X + 0.589$, where X is given in degrees Celsius (Parker 1988). We did not incorporate energy expenditures associated with heat stress because animals in shaded forested habitats very rarely encountered operative temperatures exceeding critical limits (Parker 1988).

We also conducted 5 thermal trials (Jan, Mar, May, Aug, Sep 1990) to compare conditions at the weather station (located in an open area) with forested associations on the island. During each day-long trial, we monitored air temperature, wind speed, and black-globe temperature (a fast-responding thermocouple inside a black copper float that integrates temperature, wind, and solar radiation into one index) (Renecker and Hudson 1986, Parker et al. 1996). Black-globe temperature was measured in lieu of incoming solar radiation, which is highly variable under canopy environments. All thermal measurements were made simultaneously over a 1-hr period in 3 devil's club understories, followed by 3 blueberry understories and then 3 skunk cabbage understories; the entire suite of measurements was repeated again on that day. All data were compared with values logged automatically at the weather station.

Energy requirements for production by black-tailed deer were estimated to be 4.7% of basal metabolic rate (BMR) during molt and 5% of BMR during antler growth (Robbins 1983:224), after assuming the interspecific mean for basal metabolism (70 $\text{kcal} \cdot \text{kg}^{-0.75}$ [Kleiber 1947]; 1 kcal = 4.18 kJ). Energy requirements for growth of fawns (kcal/g mass gain) were estimated by $0.76\ \text{kg}^{0.37}$ (Robbins 1973). Monthly energy requirements for fetal growth (kcal retention/kg fetus) were calculated as for white-tailed deer by $e^{0.0501X - 0.8393}$, where X is the stage of gestation from zero to 100% (Robbins and Moen 1975). We estimated monthly energy demands for lactation using milk production (ml/day) and composition (kcal/ml) determined for black-tailed deer (Sadleir 1980).

Measures of Energy Expenditure

To corroborate our calculations of energy requirements, we used doubly-labeled (isotopic) water to determine the energy expenditures of free-ranging deer over a weekly period in winter and in summer of both years of the study (Jan and Jul 1989, 1990). Five animals (2 males, 3 females) were sampled in the first winter trial; 4 animals (2 males, 2 females) were sampled in winter 1990. During the first summer, 2 nonlactating females and 3 males were sampled; in the second summer, 5 females (of which 4 were lactating) were sampled.

Because the deer accepted the close proximity of researchers, urine could be collected as body water samples using a small vial attached to a 2-m pole. Following the collection of a prior-to-injection urine sample, each animal was given by syringe a weighed dose of tritiated water (^3H_2O, 11.1 GBq/ml; 1 ml/50 kg body mass; New England Nuclear Research Products, Boston, Massachusetts, USA) and a weighed dose of oxygen-18 ($H_2{}^{18}O$, 99.1–99.3 atom %; 0.2 ml/kg body mass; Isotec, Miamisberg, Ohio, USA). Urine also was collected on each of the following 5 days. Urine samples were centrifuged with activated carbon (Norit RO 0.08, Aldrich, Milwaukee, Wisconsin, USA) to remove coloration and were frozen until analyses for ^3H_2O-specific radioactivity by liquid scintillation counting (Holleman et al. 1982) at the Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska, USA. Urine samples (including initial background samples from the animals prior to injection and standard solutions to determine the exact concentration of the injected isotope) were analyzed for oxygen-18 by mass spectrometry at a commercial laboratory (Krueger Enterprises, Geochron Laboratories Division, Cambridge, Massachusetts, USA). All samples were stored in sealed thick-walled plastic vials with little air space above the sample to minimize evaporation and exchange with ambient water vapor.

We calculated CO_2 production as in Fancy et al. (1986) using equations developed by Holleman et al. (1982), which include corrections for isotopic fractionation effects (Lifson and McClintock 1966) and assume that evaporative water loss is 25% of total water loss (Cameron 1972). Changes in body mass during the isotopic trials were determined for all animals.

Statistical Analyses

We used an α level of 0.05 for statistical significance in all analyses. Because we used telemetric data to determine time spent active and inactive by black-tailed deer, we assessed the accuracy of those determinations by comparing them with visual observations. For trials (defined as the continuous behavioral and forage intake data collected for an individual deer on a single day) in which observed animals also were monitored by telemetry (965 hr of observations), we wrote a quick BASIC program to sample both the observed and telemetric data at 5-min intervals. For each trial, we determined the proportion of 5-min samples that were correctly predicted by the telemetric data, where inactivity included standing in 1 place >5 min and lying and where activity was all other behaviors.

Because we resampled the same deer during this study, we used a repeated measures ANOVA (SAS:PROC GLM; SAS Institute 1987) to examine seasonal differences in diet quality, activity patterns, and intake rates. The analysis requires that samples be obtained from each individual for each sampling interval. Data are shown for all months on all figures, but for repeated measures tests of seasonal effects, it was necessary to pool data into 9 periods: October–November, December, January, February–March, April, May, June, July, and August–September. We used linear contrasts to test for specific monthly and yearly differences. Differences between males and females for each month were analyzed with Bonferonni multiple comparisons to allow for an experimentwise error rate of 0.05. Unless otherwise noted, data are given as the mean ± SE. We used a nonlinear curve-fitting package to quantify the relation between the ratio of energy intake to requirement and changes in body mass (SAS:NLIN; SAS Institute 1987) using a Michaelis-Menton model: $Y = c + [aX \div (b + X)]$.

To assess the effects of variation in selected parameters in the energy and protein simulation models, we conducted uncertainty analyses (*sensu* Lovvorn and Gillingham 1996). We considered ranges of values likely to occur with fawn, adult male, and adult female black-tailed deer in winter and adult male and female deer in summer (Table 1), rather than evaluate the variability within a percentage of the coefficient of variation (e.g., Madenjian et al. 1993). Values for body mass, intake, percent time active, percent time foraging, snow depth, and the proportion of time spent in the thermoneutral zone were representative of the ranges encountered in this study; values for all other selected parameters were within ± 10% of reported means (*see* equations above). We were not attempting to sample from normal distributions around particular means, but to sample variation within the observed ranges. Consequently, in our uncertainty analyses we considered all parameters to be uniformly distributed within these ranges. Uncertainty simulations for the energy and protein models each included 150 runs. Using a Latin hypercube design (Swartzman and Kaluzny 1987), we divided the uniform distribution for each parameter into 150 equal intervals; for each run, values for each parameter were randomly chosen without replacement. After completing the simulations, the resulting values of the dependent variable (energy expenditure in $\mathrm{kJ \cdot kg^{-0.75} \cdot day^{-1}}$ for the energy model and protein demand in $\mathrm{g\ N \cdot kg^{-1} \cdot day^{-1}}$ for the protein model) were ranked from lowest to highest, and then the rank variable was regressed against the independent variables (the randomly chosen parameter values) for each simulation. Relative partial sums of squares (RPSS) for ranked data indicated the variance in protein or energy expenditure explained by variation of individual parameters, with effects of other parameters statistically removed (*see* Bartell et al. 1986, Swartzman and Kaluzny 1987). We thus were able to determine which parameters in each model had the greatest effect on the model predictions. For ease of interpretation, we report partial coefficients of determination (partial r^2). Parameters, however, can show high correlation, but account for small residual variances as indicated by RPSS (Bartell et al. 1986).

RESULTS

We observed black-tailed deer on Channel Island eating >70 different plant species of which most were forbs ($n = 39$; Table 2). Essentially all plants reported on the island were eaten to some extent by deer. Some plant species were eaten only opportunistically, such as Alaska yellow cedar (*Chamaecyparis nootkatensis*) that washed up on the beach of the island, or European mountain ash (*Sorbus aucuparia*) and highbush cranberry (*Viburnum edule*) that grew only on 1 extremely steep and relatively inaccessible slope of the study site. Some species were only "tested" for palatability and eaten rarely (e.g., *Picea sitchensis*). Other species were consumed depending on temporal availability. The deer avidly sought mushrooms across the island only when they were readily available in the autumn and traveled in search of windblown lichens following major wind events during winter. The selection of parts of some plant species also depended on plant phenology. For example, deer consumed the fiddleheads of *Dryopteris* ferns in early spring, the green fern fronds during spring and summer, and the rhizomes in winter. Similarly, *Alnus* catkins and buds were eaten in early spring, the

Table 1. Parameters and their ranges used in uncertainty analyses of nutritional simulation models for black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

Parameter	Winter			Summer	
	Fawn	Adult female	Adult male	Adult female	Adult male
Protein model					
Body mass (kg)	18.2–26.5	32.6–41.3	34.5–40.0	32.0–44.5	35.7–52.0
Intake rate ($g \cdot kg^{-1} \cdot day^{-1}$)	6.2–12.8	6.2–12.1	6.8–12.8	18.1–34.8	16.5–24.0
Metabolic fecal nitrogen ($g\ N \cdot kgDM\ intake^{-1}$)[a]	7.029–8.591	7.029–8.591	7.029–8.591	7.029–8.591	7.029–8.591
Endogenous urea nitrogen ($mg\ N \cdot kg^{-0.75} \cdot day^{-1}$)	0.104–0.127	0.104–0.127	0.104–0.127	0.104–0.127	0.104–0.127
Fetus growth ($g\ N\ retention \cdot kg\ fetus^{-1}$)		2.754–3.366			
Molting ($mg\ N \cdot kg^{0.75} \cdot day^{-1}$)				0.765–0.935	0.765–0.935
Lactation ($g\ protein \cdot day^{-1}$)				30.312–37.048	
Antler growth ($mg\ N \cdot kg^{-0.75} \cdot day^{-1}$)					0.27–0.33
Energy model					
Body mass (kg)	18.2–26.5	32.6–41.3	34.5–40.0	32.0–44.5	35.7–52.0
Moving metabolic rate ($kJ \cdot kg^{-0.75} \cdot min^{-1}$)	0.477–0.500	0.435–0.464	0.435–0.464	0.437–0.483	0.437–0.483
Standing metabolic rate ($kJ \cdot kg^{-0.75} \cdot min^{-1}$)	0.453–0.476	0.378–0.435	0.378–0.435	0.431–0.437	0.431–0.437
% time active	45.0–55.0	45.0–55.0	45.0–60.0	48.2–61.21	51.26–60.73
% time foraging	78.3–99.7	78.3–99.7	78.3–99.7	78.3–99.7	78.3–99.7
Snow depth (cm)	0–35	0–35	0–35		
Proportion of time in thermoneutral zone	0.7–1.0	0.7–1.0	0.7–1.0	0.6–0.8	0.6–0.8
Proportion of time below thermoneutral zone	0–0.30	0–0.30	0–0.30	0.2–0.4	0.2–0.4

[a] kgDM is kg dry matter.

Table 2. Forages consumed by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990. Forage classes are the same as those used in Figures 3, 5, and 8. The identifying number used to record each species in our study and its botanical code are presented.

Forage class and number	Code	Scientific name	Common name
Forbs			
1	COCA	*Cornus canadensis*[a]	Bunchberry dogwood
2	COAS	*Coptis asplenifolia*[a]	Fernleaf goldthread
3	RUPE	*Rubus pedatus*[a]	Five-leaf bramble
4	TITR	*Tiarella trifoliata*[a]	Trifoliate foamflower
8	MADI	*Maianthemum dilatatum*[a]	False lily-of-the-valley
9	PRAL	*Prenanthes alata*[a]	Rattlesnake root
10	STST	*Streptopus streptopoides*[a]	Twisted-stalk
11	STAM	*Streptopus amplexifolius*[a]	Twisted-stalk
19	LICO	*Listera cordata*	Heartleaf twayblade
26	CLUN	*Clintonia uniflora*	Single-flowered clintonia
29	MOUN	*Moneses uniflora*	Single delight
31	PLAN	*Plantago macrocarpa*[a]	Alaska plantain
36	POEG	*Potentilla egedii*[a]	Pacific silverweed
37	ACMI	*Achillea millefolium*[a]	Common yarrow
38	ANLU	*Angelic lucida*[a]	Seawatch angelica
39	LISC	*Ligusticum scoticum*[a]	Beach lovage
40	RANU	*Ranuculus occidentalis*[a]	Buttercup
48	EQAR	*Equisetum* spp.[a]	Horsetail
61	PLMA	*Plantago maritima*[a]	Sea plantain
62	COPA	*Conioselinum pacificum*[a]	Hemlock parsley
63	GLMA	*Glaux maritima*[a]	Sea milkwort
64	DOPU	*Dodecatheon pulchellum*	Shooting star
65	FRCA	*Fritillaria camschatcensis*	Kamchatka lily
66	CAHY	*Castilleja hyetophila*	Scarlet paintbrush
67	LUNO	*Lupinus nootkatensis*	Nootka lupine
68	LAMA	*Lathyrus japonicus*	Beach pea
69	COOF	*Cochlearia officinalis*	Scurvy grass
70	VIGL	*Viola glabella*	Stream violet
71	RIBE	*Ribes laxiflorum*	Trailing blackcurrant
72	GATR	*Galium* spp.[a]	Bedstraw
73	LUNF	*Lupinus nootkatensis*	*Lupinus* flowers
79	COWP	*Heracleum lanatum*	Cow-parsnip
80	LYCO	*Lycopodium* spp.	Clubmoss
81	ASTR	*Aster* spp.	Aster
82	DOCK	*Rumex* spp.	Dock
84	CLOV	*Trifolium* spp.	Clover
86	EPIL	*Epilobium angustifolium*	Fireweed
88	SWTC	*Osmorhiza* spp.	Sweet-cicely
90	VERA	*Veratrum viride*	False hellebore
Ferns			
5	DRDI	*Dryopteris dilatata*[a]	Spreading woodfern
6	BLSP	*Blechnum spicant*[a]	Deer fern
7	GYDR	*Gymnocarpium dryopteris*[a]	Oak fern
27	POVU	*Polypodium vulgare*[a]	Licorice fern
28	ATFI	*Athyrium filix-femina*[a]	Lady fern
53	AT_F	*Athyrium filix-femina*[a]	*Athyrium* fiddleheads
54	DRFI	*Dryopteris dilatata*[a]	*Dryopteris* fiddleheads
Skunk cabbage			
12	LYAM	*Lysichiton americanum*[a]	Yellow skunk cabbage
52	LY_C	*Lysichiton americanum*[a]	*Lysichiton* centers
Devil's club			
13	OPHO	*Oplopanax horridus*[a]	Devil's club
77	OP_F	*Oplopanax horridus*	*Oplopanax* flowers

(Continued on following page.)

Table 2. Continued.

Forage class and number	Code	Scientific name	Common name
Conifers			
14	TSHE	*Tsuga heterophylla*[a]	Western hemlock
15	PISI	*Picea sitchensis*	Sitka spruce
83	CEDR	*Chamaecyparis nootkatensis*	Alaska yellow cedar
Shrub leaves			
16	MEFE	*Menziesia ferruginea*[a]	Rusty menziesia
17	VAPA	*Vaccinium parvifolium*[a]	Red huckleberry
18	VAAL	*Vaccinium alaskaense* and *ovalifolium*[a]	Alaska blueberry
20	VAOX	*Vaccinium oxycoccus*[a]	Bog cranberry
23	SACA	*Sambucus callicarpa*[a]	Pacific red elder
24	RUSP	*Rubus spectabilis*[a]	Salmonberry
25	RUPA	*Rubus parviflorus*	Western thimbleberry
32	ALSI	*Alnus sinuata*[a]	Sitka alder
33	MAFU	*Malus fusca*[a]	Pacific crabapple
34	COST	*Cornus stolonifera*	Red-osier dogwood
35	RILA	*Ribes lacustre*	Bristly black currant
59	AL_C	*Alnus sinuata*[a]	*Alnus* catkins
60	AL_B	*Alnus sinuata*[a]	*Alnus* buds
78	EASH	*Sorbus aucuparia*	European mountain ash
89	CRAN	*Viburnum edule*	Highbush cranberry
Shrub stems			
56	MEFS	*Menziesia ferruginea*[a]	*Menziesia* stems
57	VAPS	*Vaccinium parvifolium*[a]	*Vaccinium parvifolium* stems
58	VAAS	*Vaccinium alaskaense* and *ovalifolium*[a]	*Vaccinium* stems
74	AL_S	*Alnus sinuata*	*Alnus* stems
75	VAPB	*Vaccinium parvifolium*[a]	*Vaccinium parvifolium* buds
76	VAAB	*Vaccinium alaskaense* and *ovalifolium*[a]	*Vaccinium* buds
Rhizomes			
55	DRRH	*Dryopteris dilatata*[a]	*Dryopteris* rhizomes
87	AT_R	*Athyrium filix-femina*	*Athyrium* rhizomes
Lichens			
22	ALEC	*Alectoria* and *Usnea* spp.[a]	Alectoria, beard lichen
45	LICG	*Lobaria* spp.[a]	
46	LICB	*Peltigera* spp.[a]	
Graminoids and sedges			
41	ELAR	*Elymus arenarius*[a]	Beach rye
42	DECA	*Deschampsia caespitosa*[a]	Hairgrass
43	HOBR	*Hordeum brachyantherum*[a]	
47	CARX	*Carex* spp.[a]	Sedge
51	CX_H	*Carex* spp.	*Carex* seedheads
Other			
21	MUSH	Mushrooms[a]	Various mushrooms
30	LIVR	*Conocephalum conicum*[a]	Liverwort
44	FUFU	*Fucus furcatus*[a]	Rockweed algae
85	MOSS		Moss
49	UNKN		Unknown
50	OTHR		Other

[a] Designates forages that were monitored to assess forage quality.

stems during winter, and the dried leaves in autumn. Other than *Carex* and *Fucus* spp., the numerous beach plants were all seasonally-dependent forbs and therefore were not eaten during winter.

Available Forage Quality and Quantity

Forages consumed by black-tailed deer were grouped for sampling and analysis into a combination of prominent botanical

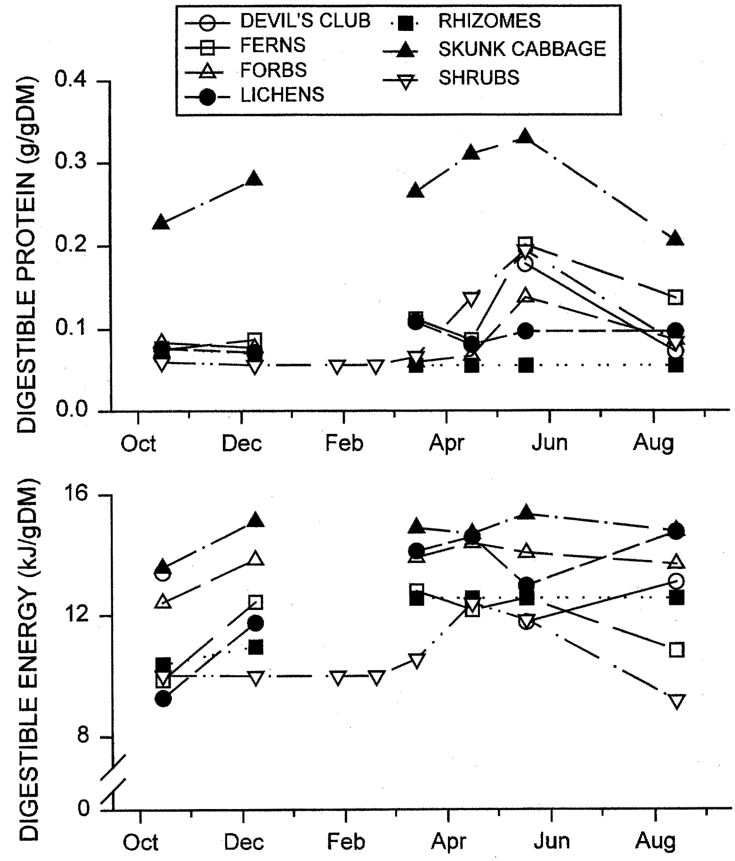

Fig. 3. Seasonal changes in apparent digestible protein and digestible energy content of major forage classes on Channel Island, southeast Alaska, between October 1988 and September 1990. Lines are used to show trends within classes.

classes (e.g., conifers, forbs), classes reflecting seasonal changes in availability (e.g., shrub stems, shrub leaves, fern foliage, fern rhizomes), and specific dietary items selected by deer in significant amounts at specific times of the year (e.g., skunk cabbage, devil's club, lichens). Therefore, the number of plant species within those forage "classes" varied depending on seasonal availability and phenological changes within a species.

Apparent digestible protein content of terrestrial, above-ground forage classes increased markedly with new leaf growth in spring (Fig. 3). Changes in protein content were relatively low in below-ground rhizomes and arboreal lichens. Skunk cabbage leaves contained significantly higher amounts of digestible protein (range = 0.25–0.33 g/g dry matter) than all other classes of forage (range = 0.06–0.20 g/g dry matter from Fig. 3; <0.01 g/g dry matter for *Tsuga heterophylla* seedlings) at all times of the year; they also showed the least seasonal variation (26% decrease from summer to winter) compared to other above-ground terrestrial groups (61.0 ± 3.4%). Prominent seasonal variations were recorded within some species (Appendix A).

Apparent digestible energy content varied seasonally within and among forage groups; extremes ranged from <8 kJ/g dry matter in shrubs during early winter to >15 kJ/g dry matter in newly emerging skunk cabbage centers (Fig. 3). Nonshrub forages, excluding arboreal lichens that were available only after windfall events, provided only 15.1 ± 4.6% less digestible energy during winter than in summer months. Least seasonal variation was observed in skunk cabbage (7.5%, excluding analyses of midveins). Winter values for shrubs were 26% less than in summer, reflecting the availability of stems compared to leaves. Consequently, shrub stems contained the lowest digestible energy of all forage classes during winter. Hemlock seedlings averaged 11.6 kJ/g dry matter. When vegetation data were collected during January and February, shrubs and conifers were the only forages available to deer because snow covered the herb layers. As with digestible protein, seasonal variations occurred in digestible energy within individual species (Appendix B).

Direct comparisons of availability between shrub and nonshrub classes were not possible because shrub biomass was estimated as percent cover and nonshrub classes were recorded as dry mass equivalents (plant units). Deciduous shrub cover, including leaves and/or stems, remained relatively constant over the year and averaged 39.1% in *Vaccinium*, 13.3% in skunk cabbage, and 7.2% in devil's club communities. Abscission of leaves generally occurred in September; new buds and flowers appeared in April. Conifer seedlings and branches of larger trees covered a much smaller portion of the vegetation plots: 6.8% in *Vaccinium*, 4.8% in skunk cabbage, and 3.6% in devil's club communities. The same vegetation plots that we monitored also were sampled for vegetation profiles and biomass as part of a coastal Alaska multiresource inventory system (e.g., LaBau and Schreuder 1983, Yarie and Mead 1989). From that inventory, we determined the biomass of the shrub layer (excluding devil's club) for foliage and twigs up to 5 mm in diameter in August to be much greater than nonshrub components (c.f. Fig. 4): 402.6 g/m^2 in *Vaccinium*, 66.3 g/m^2 in skunk cabbage, and 126.4 g/m^2 in devil's club communities. Contributions of available digestible energy and protein from shrubs also were significantly greater than those for the nonshrub components (c.f. Fig. 4): 3,472 kJ/m^2 and 30.4 g protein/m^2 in *Vaccinium*, 286.7 kJ/m^2 and 3.4 g protein/m^2 in skunk cabbage, and 490.0 kJ/m^2 and 4.1 g protein/m^2 in devil's club communities.

The total dry matter, digestible protein, and digestible energy available per square meter in the vegetation plots, excluding tree and shrub components, were highest in spring (May) in all 3 understory communities (Fig. 4). Values reflected the contribution of large-sized leaves during new leaf flush (*Lysichiton* and *Oplopanax*) and, therefore, were highest in skunk cabbage areas (4.1 g dry matter/m^2, 1.0 g protein/m^2, 58.2 kJ/m^2), followed by devil's club communities (3.0 g dry matter/m^2, 0.56 g protein/m^2, 38.6 kJ/m^2), and least in predominantly *Vaccinium* areas (1.5 g dry matter/m^2, 0.26 g protein/m^2, 20.9 kJ/m^2). Availability of specific forage classes varied within community and season. For example, lichens were most available in *Vaccinium* communities; fern rhizomes were most abundant in devil's club communities. Both quantity and quality of forbs increased throughout summer (May–Aug), while the contributions of skunk cabbage to available forage biomass declined markedly (in response to consumption by deer). In January and February, the herb layer, which consisted of 4 winter-green forbs (*Cornus canadensis*, *Coptis asplenifolia*, *Rubus pedatus*, *Tiarella trifoliata*) and 1 fern (*Blechnum spicant*) was generally covered in snow except in isolated patches and effectively unavailable to deer in all 3 communities.

Dietary Composition and Quality

The herb-layer forages (forbs, ferns, and skunk cabbage) composed the largest component of dry matter intake by black-tailed deer during all months except January, February, and March (Fig. 5). This layer ranged between 41 and 46% of the diet in September, November, December, and April and between 55–58% in August and October. In midsummer, the herb-layer forages composed an even greater portion of the diet selected by deer: 69–74% during May through July. Animals also ate large quantities of deciduous shrub leaves throughout the summer; in September

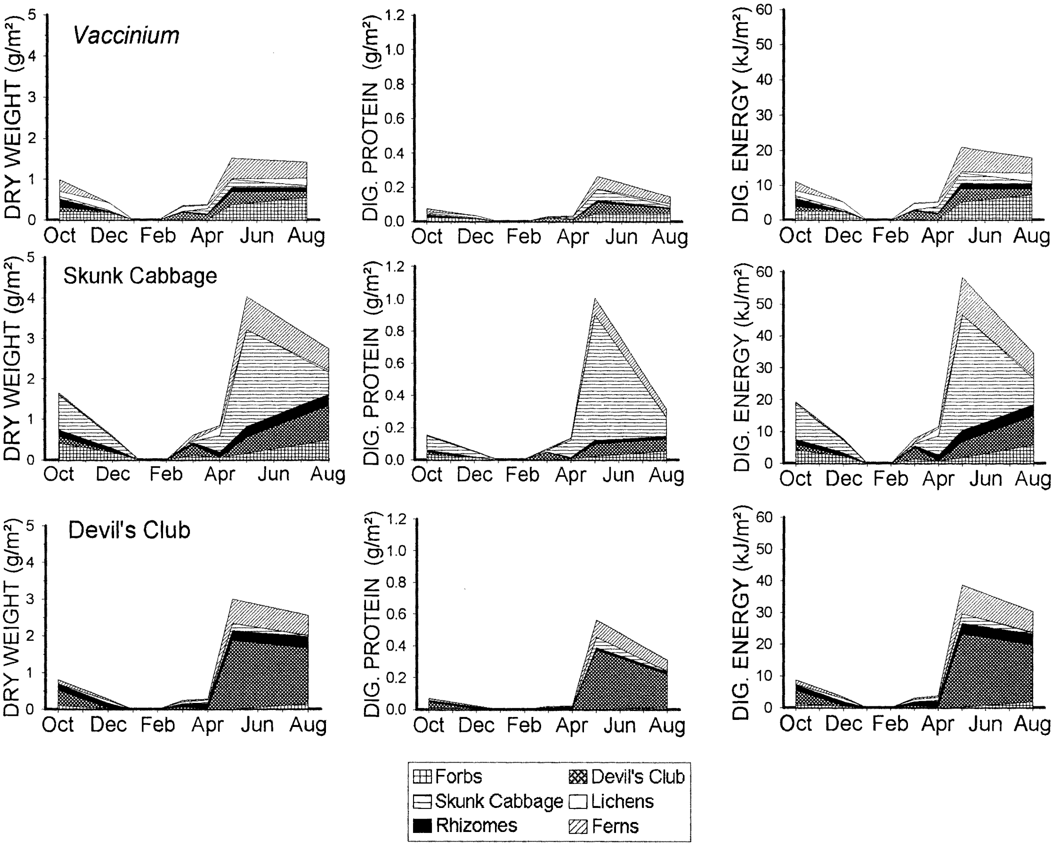

Fig. 4. Availability of nonshrub forage biomass, apparent digestible protein, and apparent digestible energy in the 3-plant-understory associations (*Vaccinium*, skunk cabbage, and devil's club) on Channel Island, southeast Alaska, between October 1988 and September 1990.

they consumed large amounts of fallen leaves (*Malus* and *Alnus* spp.). During midwinter (Jan–Mar) when herb-layer forages were covered in snow and contributed only 8% of the diet, deer primarily ate deciduous shrub stems and some conifer foliage. Shrub and conifer consumption was highest at 65% of the diet in January, declining to 42–47% in February and March.

Two other forages were eaten in significant amounts by black-tailed deer during the winter: arboreal lichens and fern rhizomes (Fig. 5). During February and March, lichens (*Alectoria* and *Usnea* spp.) composed more than one-third of the dry matter intake (34–35%). *Dryopteris* rhizomes were temporarily available to the animals in winter and early spring when the ground was not hard-frozen or deep snow-covered; during the second year of the study, they composed 30% of the December diet.

The dietary crude protein selected by our animals, as calculated from the relative amounts of individual species within mixed diets, showed extreme seasonal variation, ranging from a low of 8.0% in February to a high of 31.3% in June (Fig. 6; $P < 0.001$). After correcting for digestibility and biological values, the net protein available to the animals in their selected diets was much lower: 2.0% in February and 10.8% in June. The average gross energy content of the diets selected by black-tailed deer also varied significantly with

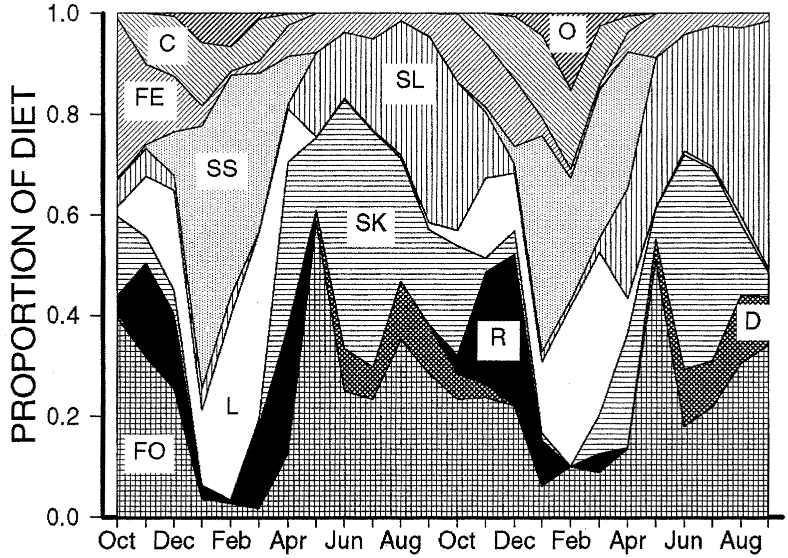

Fig. 5. Seasonal changes in the proportion of the diets consumed by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990, as represented by prominent forage classes: forbs (FO), ferns (FE), fern rhizomes (R), skunk cabbage (SK), devil's club (D), conifers (C), shrub leaves (SL), shrub stems (SS), lichens (L), and other (O) miscellaneous forage items noted in Table 2.

month ($P < 0.001$). In contrast to crude protein, the highest dietary gross energy values occurred in winter (Jan: 20.36 ± 0.29 kJ/g dry matter) when the selected diets averaged 14.4% coniferous forage, which contains large amounts of high energy volatile oils; the lowest dietary gross energy was in late September–early October (18.43 ± 0.06 kJ/g dry matter). After correcting for digestibility and metabolizability, the energy content available to the animals was lowest in January (8.70 ± 0.09 kJ/g dry matter) and highest in June (11.77 ± 0.44 kJ/g dry matter). No significant differences in dietary protein or energy content occurred between the 2 years of the study or between the diets chosen by males and females ($P < 0.001$).

Daily Activity Patterns

Telemetric data for black-tailed deer correctly predicted 95.7 ± 0.004% ($\bar{x} \pm$ SE) of active and inactive behaviors ($n = 165$ trials). Therefore, these data were used for estimates of activity in all analyses.

The average amount of time spent active by all black-tailed deer on Channel Island was 51.0% (SD = 2.78%) of the day, with no significant differences between years or sexes (Fig. 7). Significant variation did occur between months ($P < 0.001$); animals were least active in February 1990 (44.7 ± 7.1%) and most active during September 1990 (56.6 ± 7.9%). The coldest winter conditions of the study occurred during that February, and activity levels during that summer likely reflected the need to replenish body reserves following the high energetic demands of lactation for 4 of the 5 females and the onset of rut for males. When data were grouped by season (winter = Oct–Mar, summer = Apr–Sep), the amount of time spent active (averaged for all 9 animals in the last year of the study) was significantly less in winter (50.2%) than in summer (53.6%; $P = 0.044$). Foraging averaged 91.9 ± 2.9% of active time, with no differences attributed to season, year, or sex as determined by repeated measures.

Quantification of Nutrient Intake

We calculated daily forage intake by black-tailed deer using estimates of the

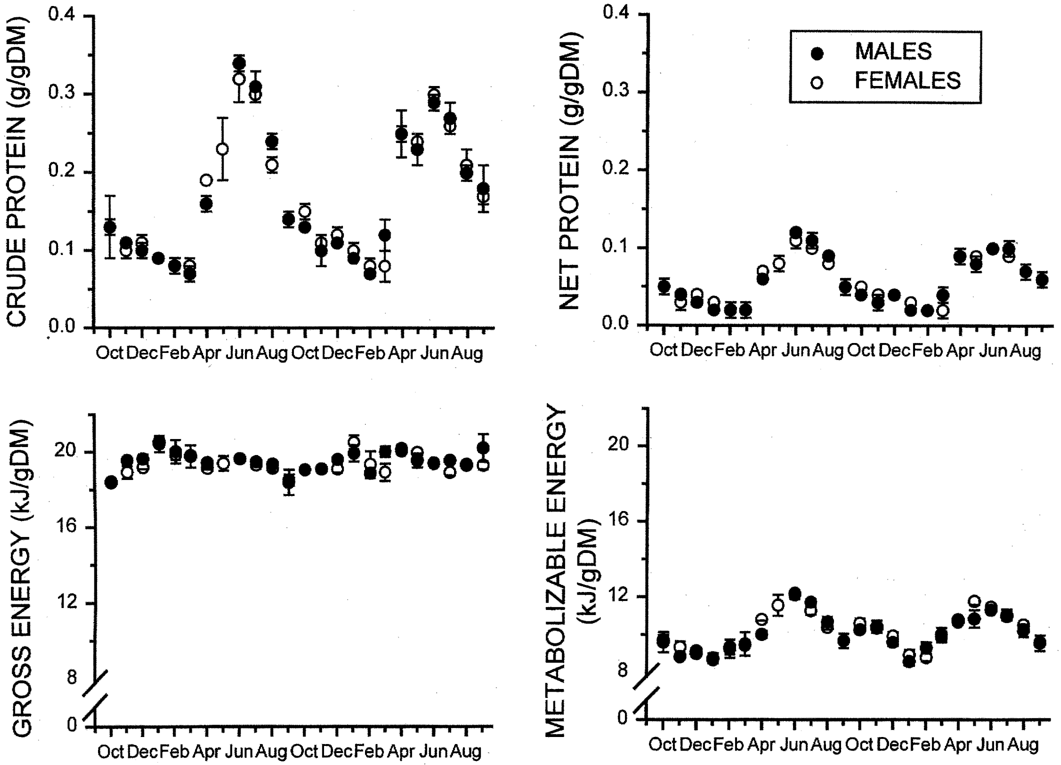

Fig. 6. Seasonal changes in crude and net protein, and gross and metabolizable energy contents of the diets consumed by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

amount of time spent active and foraging during a day by each individual animal and its respective rate of forage intake from observations. Daily dry matter intake by black-tailed deer was highest in June (28.59 ± 2.17 g dry matter$\cdot$kg$^{-1}\cdot$day^{-1}) and more than 3 times greater than the lowest average monthly values recorded during the study in November 1988 (8.05 ± 0.63 g$\cdot$kg$^{-1}\cdot$day^{-1}) and the winter values of February 1989 (9.14 ± 0.25 g$\cdot$kg$^{-1}\cdot$day^{-1}) and December 1989–January 1990 (9.43 ± 0.44 g$\cdot$kg$^{-1}\cdot$day^{-1}) (Fig. 8). Significant differences ($P = 0.039$) occurred between males and females during autumn (Oct 1989 and Sep 1990); females consumed 1.5–2.1 times more dry biomass on a per-kg-per-day basis than did males. Individual extremes in intake ranged from <200 g/day on several days in midwinter 1989 to >2,000 g/day in June 1990. Daily intake (kg/day), as a percentage of body mass, averaged 1.0 ± 0.3% in winter and 2.5 ± 0.5% in summer; highest values were recorded for lactating females (maximum = 3.8%). Highest levels of intake by forage class were recorded in June for the herb layer (20.51 g$\cdot$kg$^{-1}\cdot$day^{-1}). Daily intake of arboreal lichens was surprisingly high during late winter (Mar: 6.58 g$\cdot$kg$^{-1}\cdot$day^{-1}).

Rates of nutrient intake also varied seasonally ($P < 0.001$). During observation periods, the highest intake rates of net protein and metabolizable energy by black-tailed deer generally occurred in June of both years (0.004 ± 0.0008 g protein$\cdot$kg$^{-1}\cdot$min^{-1}; 0.457 ± 0.058 kJ$\cdot$kg$^{-1}\cdot$min^{-1}) (Fig. 9). During summer, intake rates of protein increased more than 10 times over winter (0.0004 g protein$\cdot$kg$^{-1}\cdot$min^{-1}); rates of energy intake were almost 4 times higher than rates during January (0.118 ± 0.008 kJ$\cdot$kg$^{-1}\cdot$min^{-1}). No significant differences between sexes over the 2-year period were

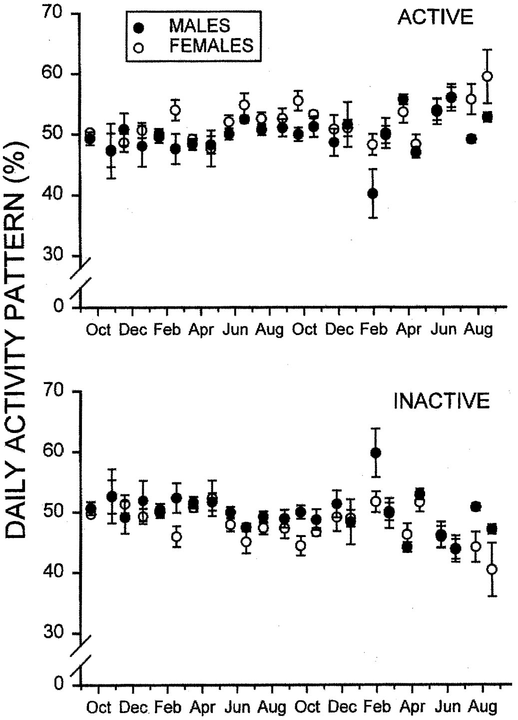

Fig. 7. Seasonal changes in the daily activity patterns of black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

identified using repeated measures analyses, although females averaged higher intake rates than males in April of both years.

Effects of Ambient Conditions on Energy Requirements

The first winter (1988–89) was generally characterized by more prolonged deep snows and extended periods of cold temperatures than the second winter. Spring arrived later in the first year than in the second, as noted by the lower forage intake rates in April (*see* Fig. 8). During the first year, average snow depths on Channel Island were greatest in early winter (Jan; 29.6 ± 6.4 cm) and gradually declined until snow disappeared in the first week of April (Fig. 10). In the second year, snow depths were much more temporally variable, reaching a maximum in mid-February of 58.4 ± 18.8 cm, but decreasing rapidly in the 3 days following this snow event. Excluding this short-lived event, maximum snow depths averaged over both years (29.6 cm) on Channel Island would increase the energy cost of travel per unit distance ($kJ \cdot kg^{-1} \cdot km^{-1}$) for an average-sized deer (winter body mass = 39 kg; relative sinking depth = 63.8% of leg length) by 325% above the expenditures for moving on bare ground (Fig. 10; *see* Parker et al. 1984). Although the 24 snow-sampling stations were not explicitly placed to determine differences between the understory communities, snow depths following snow events reflected topographical conditions and, therefore, were greatest in skunk cabbage plots (associated with lowland pockets) and least in devil's club areas (usually found on steep slopes).

Air temperatures in the forest (Y) were typically within 1 C° of the air temperature at the weather station (X) ($Y = 0.932X - 0.895$; $r^2 = 0.97$). Black-globe temperature (X) at the weather station was directly related to the operative temperature (Y) calculated for black-tailed deer using simultaneous measurements of air temperature, wind speed, and solar radiation ($Y = 1.07X - 1.72$; $n = 7{,}355$; $r^2 = 0.93$). However, black-globe temperatures in the forest (Y), representing an index of what is experienced by the animals, were less than those recorded at the weather station (X) ($Y = 0.693X - 1.445$; $r^2 = 0.91$). This difference would be greatest at high air temperatures, when the weather station received full sunlight in contrast to most forested habitats. Nonetheless, in our model we elected to use the operative temperatures determined at the weather station without correction factors to conservatively estimate supplemental energy expenditures associated with thermoregulation. Animals were able to behaviorally select their thermal conditions within a very heterogeneous environment. During winter they could have selected a thermal environment with sunlit conditions, which would have been improved over that indicated by our black-globe measurements of forested areas.

During the same time as deep snows increased locomotion costs during winter,

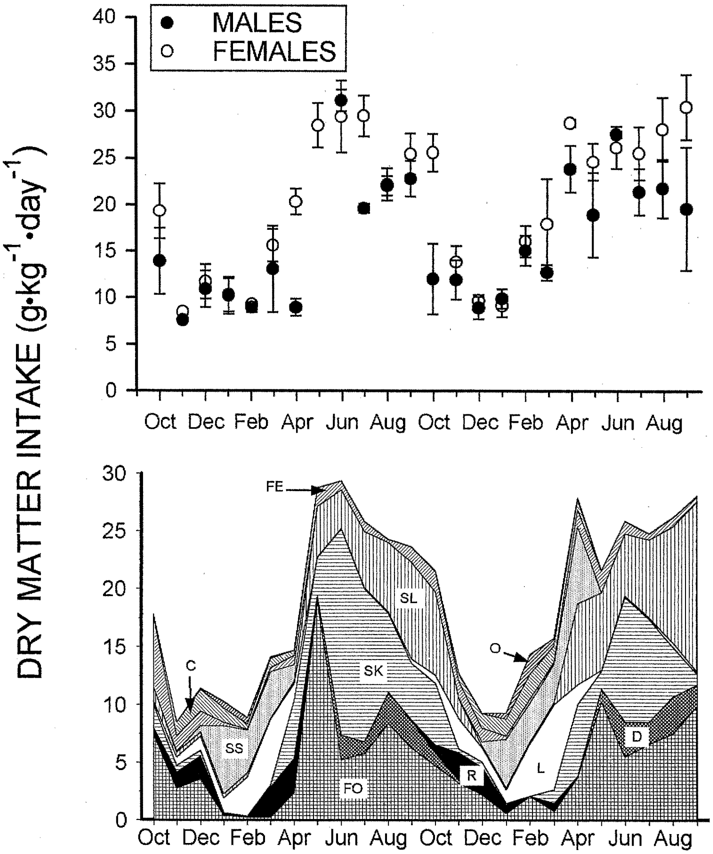

Fig. 8. Seasonal changes in daily dry matter intake by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990, as represented by prominent forage classes: forbs (FO), ferns (FE), fern rhizomes (R), skunk cabbage (SK), devil's club (D), conifers (C), shrub leaves (SL), shrub stems (SS), lichens (L), and other (O) miscellaneous forage items noted in Table 2.

thermally critical temperatures resulting in additional energy costs for thermoregulation by black-tailed deer also occurred (Fig. 11). For example, during February 1989, 39.7% of the weather observations recorded at the Channel Island weather station fell below thermally-neutral limits, resulting in average energy costs that were an additional 7% above the cost of standing. Unlike increases to locomotion costs, however, supplementary thermoregulatory expenditures also occurred during summer. Indeed, an even greater proportion of temperatures were associated with thermal stress in summer than in winter (e.g., 51.2% in June 1990, increasing energy costs of standing >5%). These results are further conservative, because the effects of rain are not included in the calculation of operative temperature. Highest average amounts of rain were recorded in November (>290 mm), but rainfall also was significant during summer months (>100 mm) and could have increased the energy costs associated with cold temperatures substantially, particularly in June with the transition from winter to summer pelage (Parker 1988).

Daily Nutrient Intake in Relation to Requirements

The estimated daily intake of net protein varied from 13- to 16-fold between

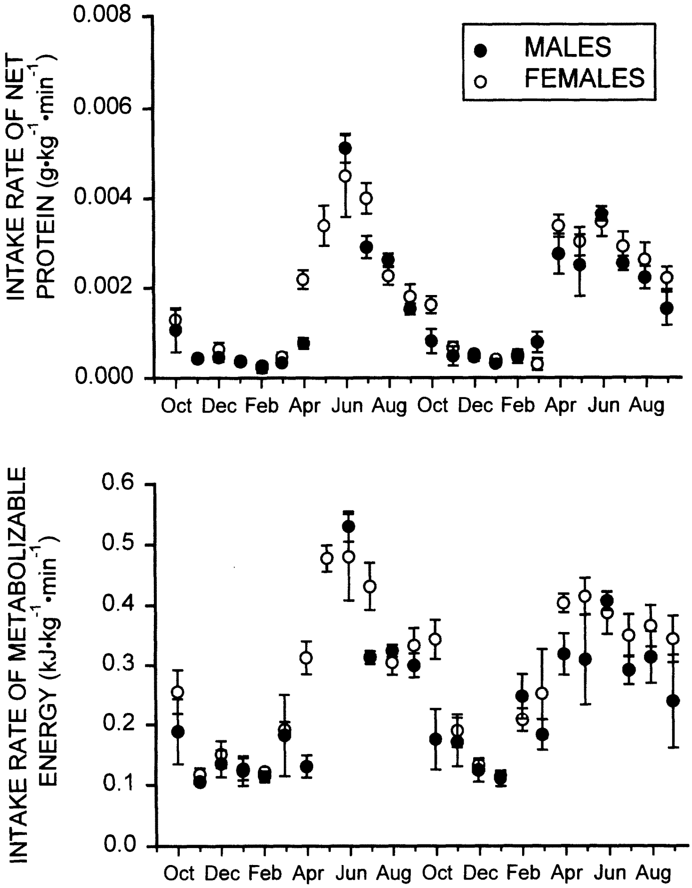

Fig. 9. Seasonal changes in the rates of net protein and metabolizable energy consumption by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

winter and summer (Fig. 12). Daily protein intake remained above calculated daily requirements for males and females during all times of the year, except during February when intake was equivalent to demands for females gestating a single fawn (0.16 g protein·kg^{-1}·day^{-1}) and just slightly less than that needed by females gestating twin fawns (0.17 g protein·kg^{-1}·day^{-1}). In contrast, daily metabolizable energy intake varied only 4-fold between June and midwinter (Jan–Feb), and animals were unable to meet calculated energy requirements for at least half the year. For adult males, intake of metabolizable energy fell below energy requirements during October–March; energy balance during the transitional months between winter and summer seasons (Sep and Apr) varied with year; and intake exceeded requirements between May and August. Metabolizable energy intake by adult females was not sufficient to meet energy requirements during November–March. Whether energy demands were met in April and October depended on yearly variations in spring green-up and leaf abscission. For females nursing twin fawns, energy balance also was always negative between June and August; females with single fawns were close to or just under meeting calculated requirements during the same summer months. All females met or exceeded energy demands in May and September.

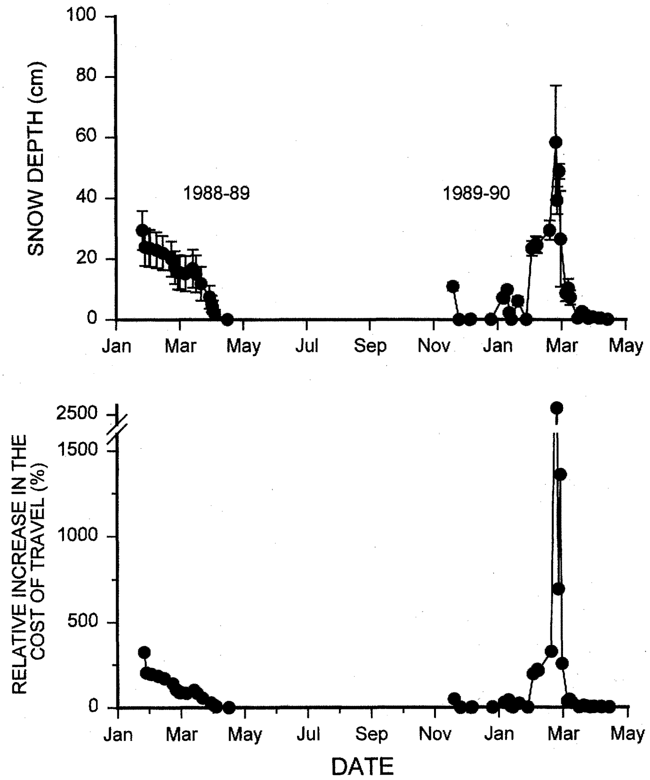

Fig. 10. Average snow depths on Channel Island, southeast Alaska, during winters 1988–89 and 1989–90 and the corresponding increase in the energy cost of travel per unit distance by black-tailed deer as a percentage above the cost of walking on bare ground.

Implications for Changes in Mass

The ratio of observed energy intake (metabolizable kJ·kg^{-1}·day^{-1}) to estimated energy requirements (kJ·kg^{-1}·day^{-1}) was directly related to changes in body mass of the individual black-tailed deer on Channel Island (Fig. 13). In general, gains in mass were highest in summer when the efficiency ratio (intake/requirement) was highest; changes in mass were negative during winter. We did not use data from April and May, when metabolic rates were likely changing between seasons and females gained significant mass prior to parturition, or in September–October, when seasonal changes in metabolism also occurred and foraging intake by males varied in response to rutting behavior. Slight deviations from the above relationship occurred for lactating females (for which mass may not have been representative, depending on the time of last nursing) and for rutting males when activity levels were greatly elevated. Those values were excluded from the regression analysis.

Uncertainty Analyses of Nutritional Models

Uncertainty analyses of 8 parameters in our model calculating energy requirements indicated that during winter, changes in snow depth had the greatest effect on our ability to predict daily energy expenditures for black-tailed deer of all ages (Table 3). Metabolic rates associated with movements by adult animals and body mass of fawns ranked second in affecting predictions. Variation in the percent of time spent foraging and costs associated with thermoregulation either were insig-

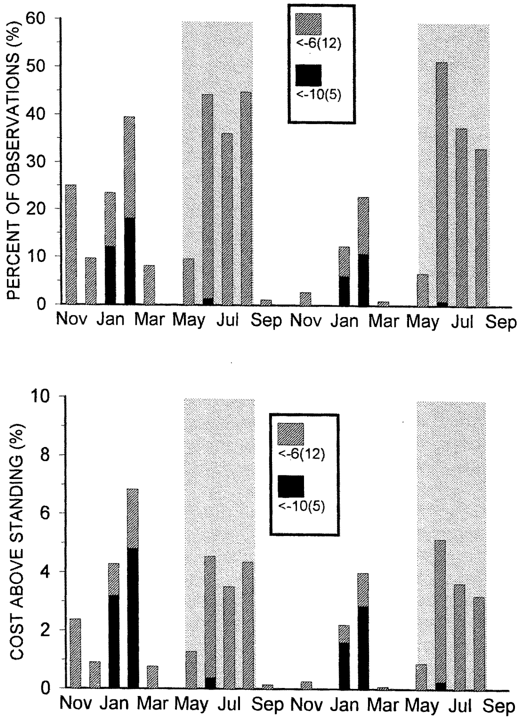

Fig. 11. Percent of time between October 1988 and September 1990 when thermal conditions on Channel Island, southeast Alaska, fell below lower critical limits for black-tailed deer and the resultant increase in energy expenditures above the cost of standing in a thermally neutral environment. Temperature strata are presented as increments below lower critical temperature (−6 to −10 C°, −10 to −20 C° in winter; summer strata are in parentheses: 5 to 12 C°, 0 to 5 C°). Background shading highlights periods when deer were in summer pelage.

nificant or had minor influence on model calculations of energy expenditure (all partial $r^2 < 0.02$, Table 3). During summer, variation in body mass and expenditures associated with movement most affected our predictions of energy requirements for adult animals.

Uncertainty analyses of the model calculating protein requirements resulted in a consistent ranking of parameters among fawns, adult males, and adult females (Table 4). In descending order, variation in intake rate, metabolic fecal nitrogen, body mass, and endogenous urinary nitrogen most affected protein requirements during winter. The same first 3 values also had the greatest influence on our predictions for summer.

Doubly-labeled Water Estimates of Energy Expenditure

Estimates of energy expenditures for black-tailed deer in winter averaged 279 ± 47 $kJ \cdot kg^{-1} \cdot day^{-1}$ ($\bar{x}$ ± SD; 648 ± 80 $kJ \cdot kg^{-0.75} \cdot day^{-1}$) in 1989 and 329 ± 26 $kJ \cdot kg^{-1} \cdot day^{-1}$ (799 ± 73 $kJ \cdot kg^{-0.75} \cdot day^{-1}$) in 1990. Air temperatures during the week-long trial in January 1989 ranged from −6 to +3 C° (the thermal index of operative temperature [T_e] = −6.2 to 0.7 C°); snow depths averaged <9 cm in forested areas. In contrast, the second winter trial in January 1990 was characterized by continuous snowfall (20 cm of new snow in open areas), high winds (up to 15 m/sec), and air temperatures of −16 to +2 C° (T_e = −16.5 to −6.1 C°). Estimates of energy expenditures during summer were highly variable and unrealistic, ranging from −23 $kJ \cdot kg^{-1} \cdot day^{-1}$ (−55 $kJ \cdot kg^{-0.75} \cdot day^{-1}$) in the first summer to +1,672 $kJ \cdot kg^{-1} \cdot day^{-1}$ (+4,286 $kJ \cdot kg^{-0.75} \cdot day^{-1}$) for a lactating animal in the second summer.

DISCUSSION

As reported from syntheses of independent nutritional studies, foraging by black-tailed deer was the predominant activity within active bouts, and the amount of time spent active per day varied little throughout the year. Nonetheless, intake rates of metabolizable energy and net protein varied dramatically between summer and winter in response to the seasonal changes in forage availability.

Forage Availability and Diet Breadth

The black-tailed deer on Channel Island showed plasticity in the diet eaten as a consequence of forage constraints, as well as a pronounced selection for specific forage resources. During winter before major snow events (Nov–Dec), animals continued to select a high proportion (41–46%) of highly digestible ferns, forbs, and the occasional skunk cabbage, even though the number of forb and fern species declined seasonally from 44 to 6 and shrub stems

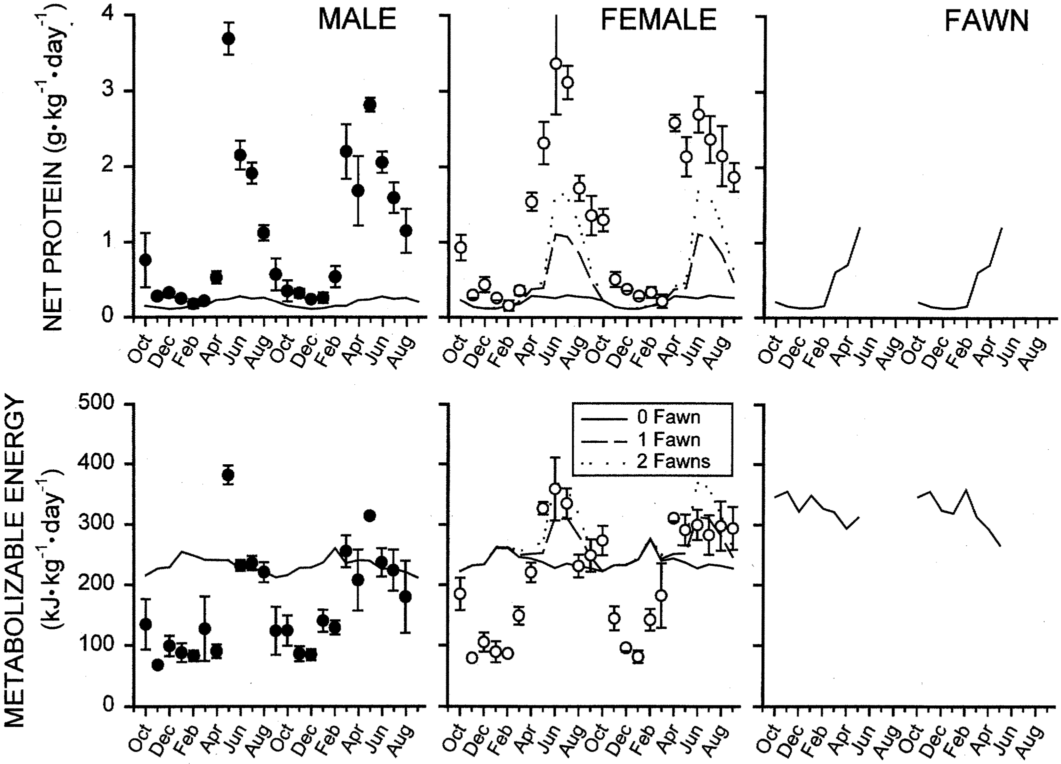

Fig. 12. Seasonal changes in daily energy and protein intake by adult black-tailed deer on Channel Island, southeast Alaska, in relation to estimated energy and protein requirements between October 1988 and September 1990. Symbols are for intake; lines are for requirements.

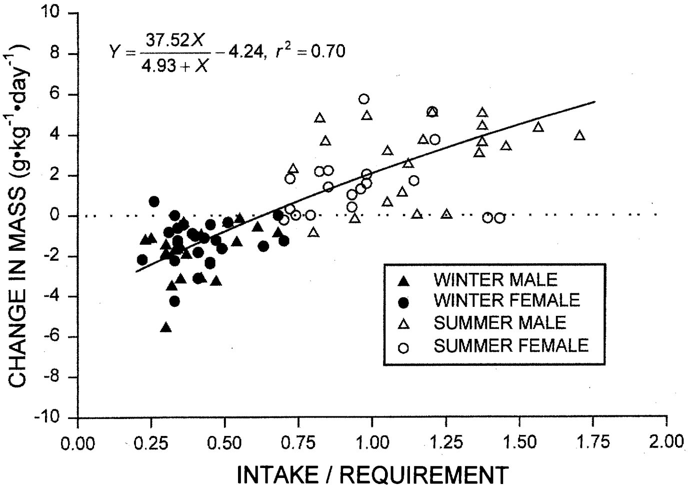

Fig. 13. Changes in body mass of black-tailed deer on Channel Island, southeast Alaska, in relation to the ratio of energy intake to energy requirement in winter and summer between October 1988 and September 1990.

Table 3. Partial coefficients of determination (r^2) using the Latin hypercube method for the results of the uncertainty analyses of energy simulation models for black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990. Blank values indicate that the parameter was not present in a specific run of the uncertainty analysis.

	Partial coefficients of determination (r^2) and rank of RPSS[a]									
	Winter						Summer			
	Fawn		Adult female		Adult male		Adult female		Adult male	
Parameter	r^2	Rank	r^2	Rank	r^2	Rank	r^2	Rank	r^2	Rank
Body mass (kg)	0.755	2*	0.579	4*	0.424	5*	0.990	1*	0.981	1*
Moving metabolic rate ($kJ\cdot kg^{-0.75}\cdot min^{-1}$)	0.715	3*	0.721	2*	0.666	2*	0.889	2*	0.952	2*
Standing metabolic rate ($kJ\cdot kg^{-0.75}\cdot min^{-1}$)	0.387	4*	0.705	3*	0.536	4*	0.001	5	0.001	6
% time active	0.319	5*	0.335	5*	0.597	3*	0.758	3*	0.759	3*
% time foraging	0.018	6	0.020	8	0.003	8	0.027	4*	0.073	4*
Snow depth (cm)	0.852	1*	0.897	1*	0.834	1*				
Proportion of time in thermoneutral zone	0.000	8	0.120	6*	0.023	6	0.001	6	0.008	5
Proportion of time below thermoneutral zone	0.000	7	0.037	7*	0.020	7				

[a] Represents the order (highest to lowest) of the relative partial sums of squares (RPSS) for each analysis.
* $P < 0.05$.

Table 4. Partial coefficients of determination (r^2) using the Latin hypercube method for the results of the uncertainty analyses of protein simulation models for black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990. Blank values indicate that the parameter was not present in a specific run of the uncertainty analysis.

	Partial coefficients of determination (r^2) and rank of RPSS[a]									
	Winter						Summer			
	Fawn		Adult female		Adult male		Adult female		Adult male	
Parameter	r^2	Rank	r^2	Rank	r^2	Rank	r^2	Rank	r^2	Rank
Body mass (kg)	0.761	3*	0.764	3*	0.743	3*	0.941	1*	0.880	3*
Intake rate ($g\cdot kg^{-1}\cdot day^{-1}$)	0.922	1*	0.958	1*	0.953	1*	0.819	2*	0.908	2*
Metabolic fecal nitrogen ($g\ N\cdot kgDM\ intake^{-1}$)[b]	0.891	2*	0.950	2*	0.949	2*	0.777	3*	0.964	1*
Endogenous urea nitrogen ($mg\ N\cdot kg^{-0.75}\cdot day^{-1}$)	0.171	4*	0.186	4*	0.233	4*	0.037	5*	0.317	4*
Fetus growth ($g\ N\ retention\cdot kg\ fetus^{-1}$)			0.020	5						
Molting ($mg\ N\cdot kg^{-0.75}\cdot day^{-1}$)							0.003	6	0.041	5*
Lactation ($g\ protein\cdot day^{-1}$)							0.766	4*		
Antler growth ($mg\ N\cdot kg^{-0.75}\cdot day^{-1}$)									0.039	6*

[a] Represents the order (highest to lowest) of the relative partial sums of squares (RPSS) for each analysis.
[b] kgDM is kg dry matter.
* $P < 0.05$.

were much more readily available. Emergent skunk cabbage centers were eaten whenever they were encountered (K. L. Parker and M. P. Gillingham, co-authors, personal observations). Following snow events, the primary components in the diet were shrubs (*Vaccinium* spp.) extending above the snow surface and hemlock seedlings growing along the tops of nurse logs. Animals rarely consumed the branches of older hemlock trees even when they were within reach. They occasionally mouthed the fallen branches of spruce (*Picea sitchensis*), but consumption was rare—in contrast to observations from high density deer populations (Lewis 1992).

The deer on Channel Island appeared to choose additional food items to augment energy intake in winter that were not eaten extensively during summer. They often spent entire foraging bouts searching for and finding lichens (*Alectoria* and *Usnea* spp.) that were blown from the tree tops. This strategy was particularly evident following wind storms, when the animals traveled to parts of the island that were dominated by *Vaccinium* communities under old coniferous canopies where lichens were most common and that were most exposed to coastal winds. Given that lichens composed 34% of the midwinter diet (average total intake in Feb = 11.8 $g{\cdot}kg^{-1}{\cdot}day^{-1}$; Fig. 9) and assuming an average digestible energy content of 12.9 kJ/g dry matter (Fig. 3), which is 30% more than contained in shrubs, an average-sized deer (winter mass = 39 kg) would have had to consume the equivalent of 200 g dry matter of shrubs to meet the same energy consumption. That additional biomass of shrubs is approximately 36% more than the animals already were consuming, and likely not temporally or physiologically possible given the digestive constraints of a slower rate of passage associated with high fiber material and rumen fill. This comparison of food types of different quality (digestibility), however, does not take into account relative sizes of the bites of the 2 different forages, which may affect the time required for foraging, or differences in protein acquisition.

During foraging bouts in early and late winter when the ground surface was not impenetrable due to ice or deep snow, black-tailed deer avidly sought the rhizomes of *Dryopteris dilatata*. The deer rooted a small opening in the soil under the dried brown fern fronds and were able to tear the entire, or a portion of, rhizome from the ground. The deer never rooted through snow for any buried forage. Fern rhizomes provided a high energy bundle (11.3 ± 0.9 digestible kJ/g dry matter), again in contrast to shrubs. Rhizomes of *Athyrium filix-femina*, which were near the soil surface and plentiful on Channel Island, usually were ignored. In the few instances when deer tried to break a portion of those rhizomes, they were unsuccessful. *Athyrium* rhizomes are much larger than *Dryopteris*, but seemed to be too hard or woody to be consumed by black-tailed deer. Use of rhizomes has been documented for other ungulates, including mountain goats (*Oreamnos americanus*) that feed on *Athyrium* during winters without snow accumulation (Klein 1953, Hjeljord 1971, Fox et al. 1989). A similar strategy for selecting bulbs of lilies was reported for gazelles in the Negev desert (Ward and Saltz 1994). Deer on Channel Island also supplemented the diet obtained in the forested communities with *Fucus* sp. found on beaches at low tide. *Fucus* contained low to moderate levels of digestible energy (8.96 kJ/g dry matter) and high levels of digestible protein (0.084 g/g). Use of seaweed to provide dietary needs has been reported for coastal populations of white-tailed deer, red deer (*Cervus elaphus*), and black-tailed deer (Clutton-Brock et al. 1982, Hanley and McKendrick 1985, Applegate and Gray 1995). We did not observe our animals consume marine brown algae drift (*Nereocystis luetkeana*), as noted for deer on the outer islands of southeast Alaska (Lewis 1992).

During the seasonal transition months of April–May and September–October, animals on Channel Island employed other selective foraging behaviors. They made use of the beach fringe communities to obtain high energy *Alnus* buds and catkins in early spring, often traveling along beach logs to reach into the shrub canopies. They consumed the new shoots of beach grasses and sedges, which emerged earlier than many of the herbs in forested communities because the ocean tides removed most snow accumulations. During autumn, deer searched for fallen leaves from *Malus* shrubs in the beach fringe areas and for numerous mushroom species located throughout the forested communities. In summer, our records of the forages consumed by black-tailed deer on Channel Island (Table 2) show the extreme dietary flexibility of this species in the coastal ecosystem and substantially expand the lists of plant species reported to have been eaten (e.g., Hanley 1984).

Rates of Nutrient Intake

Intake rates by black-tailed deer increased markedly in response to new leaf flush in spring to a maximum rate corresponding closely with maximum forage availability (Figs. 4, 9). As total availability declined during summer, so did intake rates, which reached lowest levels after leaf abscission. Typically, changes in the rates of protein intake were much greater than were changes in the rates of energy intake, corresponding with the marked changes in digestible protein content (Fig. 3; Langvatn and Hanley 1993).

Greatest intake rates during foraging bouts occurred when deer consumed large bites of skunk cabbage and devil's club. These 2 species contributed the largest proportion of the diet during April, June, and July during both years of our study. Skunk cabbage was eaten in all months of the year except January and February when new shoots were buried by snow; devil's club was consumed during all months that leaves were present. This is in contrast to general beliefs involving defense mechanisms against herbivory, i.e., that deer avoid skunk cabbage after the leaves unfurl coinciding with the increase of oxalates in the leaf tissue, and that stems and maturing leaves of devil's club are protected enough by dense spines to inhibit grazing by deer (Klein 1979). The importance of skunk cabbage as a preferred forage species has been noted by others; use of this plant may start as early as late January in mild winters (Shishido 1986) and contribute as much as 69% of the diet during summer (Hanley et al. 1985). The highest intake rates of skunk cabbage sustained during foraging bouts that we observed in free-ranging black-tailed deer approached the short-term maximums achieved by captive animals (Spalinger et al. 1988, Gillingham et al. 1997). The high selection for skunk cabbage is not unreasonable, because it fulfils most of the requirements of being a preferred forage: high abundance, large bite size (therefore, high intake rate), and high nutrient concentration. Its defensive chemistry likely dictates that it is mixed with other foods in the diet of deer.

Other work on deer in north–temperate ecosystems theorized that increased energy demands during winter could be met by increasing food intake (Wallmo et al. 1977). However, the quality of forage available in winter declines with increasing fiber content. In some species such as elk (*Cervus elaphus*) and mountain sheep (*Ovis canadensis*), passage rates and subsequently intake are constrained by a limited gut capacity; others such as mule deer may be capable of increasing gut fill to accomodate reduced digestibility (Baker and Hobbs 1987). Consumption rates by kudu (*Tragelaphus strepsiceros*) were not influenced by changing food abundance during the winter dry season in tropical savanna ecosystems (Owen-Smith 1994). Instead, dietary breadth increased and daily food intake increased as animals spent more time per day active and a higher proportion of active time foraging to compensate for the decline in dietary quality. In contrast, the black-tailed deer on Channel Island showed little change in the amount of daily activity over a 2-year period (Fig. 7) or in the amount of time spent foraging (Gillingham et al. 1997), and dietary breadth decreased with declining availability of the herb layer (Fig. 4). Duration of individual foraging bouts by deer were longer during winter than summer, but the number of foraging bouts per day declined, likely in response to processing constraints. Further evidence that processing and passage rates constrain daily intake during winter was noted during our daily observations. Within lying bouts, animals ruminated for 87% of their resting time in midwinter (Dec–Feb), in comparison with 49% of the lying time during midsummer (Jun–Aug; K. L. Parker and M. P. Gillingham, co-authors, unpublished data). Even with behavioral modifications, daily consumption by deer declined 70% from summer to winter (Fig. 8). In both tropical and coastal ecosystems, therefore, browsing animals preferred highly nutritious forb leaves, but changed foraging behavior in response to seasonal changes in food resources and environmental constraints.

Intake in Relation to Nutritional Requirements

Our models estimating nutritional requirements are useful for assessing the limitations imposed by food resources. Requirements were calculated using results from numerous physiological and nutritional linkages determined for *Odocoileus* species. When combined with our field observations, patterns and the relative magnitude of nutritional demands should apply to free-ranging animals.

Relative to protein requirements and the uncertainty analyses of the model, we are reasonably confident in our abilities to measure intake rates, but we had to rely on previous studies for the relationships between body mass and metabolic fecal nitrogen and endogenous urinary nitrogen. In contrast to many other ungulates on northern winter ranges (*see* Mautz 1978), black-tailed deer in a coastal environment generally were capable of obtaining a diet with adequate protein content. Dietary crude protein of 7% often has been quoted as the minimum necessary for maintenance of positive nitrogen balance (Murphy and Coates 1966) prior to muscle catabolism, whereas 16–17% crude protein is necessary for lactation demands (Verme and Ullrey 1972, Regelin 1979). The forage selected by our animals in southeast Alaska met the minimum requirements during winter (7–8%) and far exceeded demands during summer (29–34%). After assuming corrections for apparent digestibility, protein intake by the deer on Channel Island met requirements for maintenance (although *see* Hanley et al. 1989, 1991 for implications involving requirements during lactation and tannin-rich leaves in open clear-cuts). February was the time of year when animals on Channel Island were most likely to fall below protein requirements. In addition to lowest rates of forage intake, the high consumption of arboreal lichens contributed to negative nitrogen balance (even while providing large amounts of digestible energy; Appendix A). Because of the very low protein content in *Alectoria*, more nitrogen can be lost than acquired during digestive breakdown by the animal (Robbins 1987), although digestibility of other dietary constituents may be enhanced (Rochelle 1980). Further research is needed to determine whether the high protein content of forbs and shrubs in mature coastal forests of southeast Alaska, in comparison with that of interior temperate ecosystems, may allow black-tailed deer to reduce the rate of catabolism of body protein reserves (*see* Parker et al. 1993*a*) in lieu of vegetative sources and, therefore, to prolong the contribution of body stores to winter survival.

Relative to energy requirements, the uncertainty analyses of our model indicated that variation in snow depths, movement rates, and body mass most affected our ability to predict energy requirements. Because weights of the animals were obtained frequently (2–4 times per month), we are extremely confident in the measurements of body mass. Energy costs associated with activity also were well documented and varied directly with active bout duration ($r^2 > 0.94$, Parker et al. 1996). Although we monitored snow depths at specific snow stations, we are less sure of the snow depths that were encountered or selected by black-tailed deer during winter in an environment with considerable variation in microsites.

We used the doubly-labeled water technique to corroborate the model estimating metabolic requirements because it is currently considered to be the only accurate method for directly determining energy expenditures of animals in their natural environment. The premise of this technique is that the hydrogen and oxygen of the body water are labeled with ^3H_2O (or ^2H_2O) and oxygen-18 isotopes. Isotopic concentrations decline through time because of excretion, evaporation, and dilution through the input of unlabeled water (eating, drinking, and oxidative metabolism). Both isotopes are lost from the body via water; oxygen also is removed in respiratory CO_2. The difference in the fractional turnover rates of the 2 isotopes is a measure of the rate of CO_2 production, and enables a calculation of oxygen consumption and energy expenditure by the animal (Holleman et al. 1982).

In our study, the isotope technique proved useful only during winter. The isotopic trials in January of the first winter measured energy expenditures ranging from 2.0 to 2.6 times basal metabolic rate ($\bar{x}$ = 2.2 × BMR, where BMR = 293 $kJ \cdot kg^{-0.75} \cdot day^{-1}$; Kleiber 1947). During this trial, animals were often piloerected, with some shivering, and not much physical movement. During the second winter trial, energy costs were higher (2.5–3.0 × BMR; $\bar{x}$ = 2.7 × BMR), reflective of deeper snows, high winds, and cold temperatures. Foraging animals were observed to wallow in snow up to brisket height, even though snow depths measured at the snow stations averaged only 24 cm. They appeared to actively seek thermal shelter under logs or at the base of trees, but piloerection and shivering did not cease. Average energy expenditures determined using doubly-labeled water were 7% greater than the average January requirements calculated by the model during the first winter (females, 261 $kJ \cdot kg^{-1} \cdot day^{-1}$; males, 254 $kJ \cdot kg^{-1} \cdot day^{-1}$) and 23% greater than the model estimate for January 1990 (females, 276 $kJ \cdot kg^{-1} \cdot day^{-1}$; males, 260 $kJ \cdot kg^{-1} \cdot day^{-1}$).

A further underlying assumption of the doubly-labeled water technique is that the H and O measured by ^3H_2O and $H_2{}^{18}O$ turnover rates are only lost from the body as water or CO_2. However, ^3H potentially may be sequestered in the fat of animals gaining weight or exported in the milk fat of lactating animals (Lifson and McClintock 1966, Haggarty et al. 1991). Consequently, the difference in the fractional turnover rate of the 2 isotopes would be flawed, resulting in errant values of energy expenditure. This may explain the erratic results that we obtained during the summer isotopic trails. Using data from Haggarty et al. (1991), in which the errors associated with estimates of CO_2 production derived from isotopic water turnover were determined experimentally for a model animal (pig) that was rapidly gaining mass, we can calculate the percent error in the rate of CO_2 production (Y) relative to mass gain (X expressed as g/day), where $Y = 0.01138X + 0.1252$ ($n = 8$, $r^2 = 0.98$) and apply the correction factors to our estimates of daily energy expenditure by individual black-tailed deer during mass gain and/or lactation. For lactating animals, mass gain would include the change in mass of the animal plus the amount of fat exported during lactation, the latter based on the age of the neonates and estimates of milk intake (ml/day) and fat composition (%) at that age in mule deer (Carl and Robbins 1988). However, even after using these corrections for isotope sequestration in body fat and/or milk fat production, daily energy expenditures for the 10 animals in summer ranged from negative values up to almost 15 × BMR in a lactating animal. Additional research is needed to determine the applicability of the doubly-labeled water technique during summer when temperate ungulates typically gain body mass and grow antlers (sequestering CO_2 in the bone and/or antler pools and affecting ^{18}O turnover rates; Whitelaw et al. 1972), deposit fat reserves (sequestering the ^3H isotope; Haggarty et al. 1991), increase methane (CH_4) production with higher forage intake (resulting in ^{3}H losses from the body water pool; Fancy et al. 1986), and/or lactate (exporting ^{3}H with milk fat; Haggarty et al. 1991).

The precision of the calculations in our energetics model could be affected by several assumptions. The model was based on metabolizable energy because of the difficulty in accurately estimating net energy values for all forages and the efficiency of energy use during different physiological processes (C. T. Robbins, co-author, unpublished data). Overestimation of requirements would occur (1) if heat increment was lower in free-ranging animals than included in the metabolic expenditures of standing animals with access to food (Parker 1988) or (2) if free-ranging animals were energetically more efficient because of greater habituation to environmental constraints or the use of trailing during deep snow events. Requirements would be underestimated if winter weather conditions were more severe, as encountered by coastal mainland populations of black-tailed deer. The comparison with the doubly-labeled water values in winter indicates that the energy costs were greater than estimated by the model, although the time scale for the measurements must be considered. The energy expenditures determined isotopically occurred over a weekly period under specific ambient conditions, whereas the model calculated a monthly average. Nonetheless, those expenditures were similar to average eutherian values (2.3 × BMR; Robbins 1993: 159) and deer subjected to wind and cold temperatures (>2 × BMR; Holter et al. 1975, Wallmo et al. 1977), recognizing that dynamic snow conditions (e.g., year 2 of this study) increase energy costs above no-snow conditions (Parker et al. 1984, Fancy 1986).

Despite our assumptions and uncertainties, the relative magnitude of the difference between requirements and forage intake by deer (Fig. 12) and the relationship with changes in mass (Fig. 13) confirm earlier hypotheses that the availability of digestible energy is likely the principal nutritional factor limiting deer populations in forested habitats of southeast Alaska (Hanley and McKendrick 1985). During midwinter, animals were not capable of meeting daily energy demands through foraging, in contrast to June, when they exceeded demands by almost 50% (for nonreproductive individuals; Fig. 12). This study is the first to observe daily foraging behaviors by black-tailed deer during winter, but others have speculated that winter diets met less than one-half of energy needs (Hanley and McKendrick 1985, Lewis 1992) and that during severe winters 80% of individuals within deer populations have been known to starve (Reynolds 1979).

Energy demands for black-tailed deer on Channel Island during winter were increased by locomotion costs associated with snow depths and by supplementary thermoregulatory expenditures. During January and February, the average contribution of snow to daily requirements (23.42 $\mathrm{kJ \cdot kg^{-1} \cdot day^{-1}}$) during the 2 years of the study was approximately 4.7 times greater than that of cold temperatures (4.96 $\mathrm{kJ \cdot kg^{-1} \cdot day^{-1}}$). These environmental constraints (snow and cold) represented 9.2 and 1.9% of total daily energy expenditures (254.5 $\mathrm{kJ \cdot kg^{-1} \cdot day^{-1}}$), respectively. The low thermoregulation costs are reflective of the coastal environment inhabited by black-tailed deer and are in contrast to interior populations of mule deer that increase costs of thermoregulation >10 times during severe winters relative to mild ones (Hobbs 1989).

The impact of snow on the energy balance of black-tailed deer was further compounded by forage burial. However, we can compare the magnitude of decreased energy intake resulting from the loss of the available herb layer with the increased costs for travel in snow by using all data from December (no snow) and January (snow present). Other than differences in snowfall, we can assume that environmental conditions and plant biomass were similar between December and January. Coinciding with snowfall, then, animals consumed 3 times more shrubs and conifers but more than 5 times fewer forbs, ferns, and skunk cabbage in January (only 0.82 g·kg^{-1}·day^{-1}) than in December of both years (Fig. 9). Daily metabolizable energy intake was 11.2% less in January than in December (85.6 kJ·kg^{-1}·day^{-1} versus 96.5 kJ·kg^{-1}·day^{-1}). Snow depths increased energy costs in January by 8.2% over no snow conditions (248.2 kJ·kg^{-1}·day^{-1} versus 229.3 kJ·kg^{-1}·day^{-1}). In terms of the contribution of absolute amounts of energy to an individual's energy balance, snow affected energy costs to a greater extent (+18.9 kJ·kg^{-1}·day^{-1}) than energy intake (−10.9 kJ·kg^{-1}·day^{-1}). The analysis pertains only to the snow conditions on Channel Island during January and does not address the temporal progression of snow accumulation. For example, at the beginning of winter, 10 cm of snow will bury most forbs, thereby decreasing digestible energy intake; snow depths greater than average carpus height (25–30 cm) are needed to significantly increase expenditures for movement (Parker et al. 1984). Hence, intake would be affected to a greater extent than expenditure during times when snow depths are low.

It follows, therefore, that the negative energy balance of coastal black-tailed deer during winter was a direct consequence of the decrease in abundant high quality food (in particular in digestible energy content) and was aggravated by additional costs associated with snow and cold temperatures. Other models also have shown reduced forage availability and intake to be the most sensitive variables affecting energy balance in ungulates (Fancy 1986, Hobbs 1989).

Theoretically, changes in mass would be positive when intake exceeded requirements (ratio > 1.0) and negative when requirements were greater than intake (ratio < 1.0). The change in mass by black-tailed deer was not always zero when the efficiency ratio of intake to expenditure was 1.0 (Fig. 13). However, the 95% confidence interval around the predicted change in mass (−1.3 to 4.9) does encompass zero—suggestive of variation in any or all parameters, or the multiplicative nature of errors associated with averaging. For example, changes in mass and intake were extrapolated to monthly averages from bimonthly weighings, observations within foraging bouts (1–4 hr), and daily telemetric data. Seasonal changes in rumen fill as a percentage of body mass would confound the singular contribution of intake to changes in mass across the year. Animals may vary efficiency by selecting forages different from the average dietary composition or forages of different quality than the "average" plants that were chemically analyzed. Further, the mobilization of body reserves during times of deficient intake would contribute to energy "intake."

Body reserves accumulated during the summer by black-tailed deer help meet winter energy demands that cannot be met by foraging (Parker et al. 1996). Using data for body fat and protein depletion during winter for the animals in this study (Parker et al. 1993*a*) and assuming that each gram of fat and protein provides 9.4 kcal/g (39.3 kJ/g) and 5.3 kcal/g (22.2 kJ/g), respectively, we can calculate that body reserves contributed approximately 303 kcal/day (1,267 kJ/day) to energy requirements when averaged from October to March. During that period of reserve mobilization, body mass of our deer declined and use of body stores increased progressively each month through February from an average of 7.3 to 8.9 kcal·kg^{-1}·day^{-1} (30.5–37.2 kJ·kg^{-1}·day^{-1}) in females and 6.7 to 8.2 kcal·kg^{-1}·day^{-1} (28.0–34.3 kJ·kg^{-1}·day^{-1}) in males and then declined in March (8.7 kcal·kg^{-1}·day^{-1} in females; 8.3 kcal·kg^{-1}·day^{-1} in males). Use of body reserves varied temporally within and between individuals, depending on temporal changes in forage availability and quality, and reached a maximum of 770 kcal/day (3,223 kJ/day) for 1 animal during January–March 1990. Animals lost up to 30% of peak prewinter body mass during the mobilization of reserves. In January 1989, fat and protein stores yielded 25% of daily energy demands; in January 1990, they met 18% of metabolic requirements. This contribution of reserves to energy expenditures is slightly more than that determined for predator-free island populations of caribou (*Rangifer tarandus groenlandicus*) during moderate winters (14.2%; Adamczewski et al. 1993) and less than the maximum of 30% suggested for white-tailed deer (Mautz 1978). Body reserves are an extremely valuable contribution, especially considering that the equivalent dry matter intake by black-tailed deer during winter would be an additional 136 g dry matter/day (with an average dietary metabolizable energy content of 9.28 kJ/g dry matter; Fig. 6) or an additional 227 minutes spent foraging per day (with a metabolizable intake of 0.143 $kJ \cdot kg^{-1} \cdot min^{-1}$ for an average-sized 39-kg animal; Fig. 9). This is time they apparently did not have, if we assume that of the inactive lying time (49% of the day, 11.75 hr/day; Fig. 7), only 13% (1.5 hr/day) was free of rumination and potentially available for additional foraging.

In summer, the added energetic costs associated with lactation made it difficult for adult females to meet requirements, especially those with twin fawns. April–May and September–October became critical months for regaining mass. Intake rates by females prior to parturition and lactation were more than 1.5 times those of males; after lactation, they were 1.8 times higher (Fig. 8). For both sexes, though, high quality forage during summer and fall was necessary to ensure maximum fat accumulation. Animals were capable of achieving fat levels that exceeded 20% of body mass before the onset of winter (Parker et al. 1993*a*). Consequently, it appears that energy balance of black-tailed deer on Channel Island was controlled by energy intake throughout the entire year. Emphasis has been placed on the dramatic impacts of winter constraints on energy balance, but it is equally important to recognize the value of high quality, abundant forage in summer and of transitional fall and spring habitats to restore body condition and accumulate body reserves.

Importance of Habitat Mosaic

Sitka black-tailed deer use a variety of forested successional stages and plant associations in southeast Alaska (e.g., Rose 1982; Eck 1983; Schoen and Kirchhoff 1985, 1990; Yeo and Peek 1992). In winter, habitat use is concentrated in uneven-aged old-growth forests, with greater abundance and diversity of understory species and a significant reduction in snow accumulation relative to earlier successional stands (Schoen and Wallmo 1979, Hanley and Rose 1987, Kirchhoff and Schoen 1987). Western hemlock–Sitka spruce old-growth forests are preferred winter habitat (Rose 1982, Schoen and Kirchhoff 1990). They are characterized by a high frequency of small-scale disturbances (Hanley 1993) (such as windthrow or individual tree death) that allow light penetration through canopy gaps to enhance forage production in some areas while maintaining protective cover in others. The environmental heterogeneity results in a diverse mosaic of habitat associations found only in mature, uneven-aged stands. In contrast to younger stands, the habitats within old-growth forests generally provide a patchy cover of snow with lower snow depths and lower energy costs for travel, taller shrubs for browse, higher concentrations of forage crude protein, and a greater abundance of arboreal lichens that are deposited as highly digestible litterfall (Bunnell and Jones 1984, Hanley et al. 1989).

We observed the importance of this mosaic of conditions in terms of snow, forage, and cover to our study animals on Channel Island. *Vaccinium* communities provided the greatest overstory cover, the highest available shrub biomass, and the most access to highly digestible arboreal lichens during winter. After winter-green forbs were buried by snow depths of approximately 10 cm, *Vaccinium* shrubs were always available as forage above the snow depths encountered at the study site. Deer spent >70% of their time in those communities during winter. Devil's club associations were located on steep slopes with the least snow cover and the greatest abundance of nutritious fern rhizomes. Skunk cabbage communities were important as a year-round forage base (excluding periods of deep snow), particularly in spring and summer when intake rates by deer were significantly higher than in other communities. The beach fringe areas provided an additional plant community with lower snow depths and earlier spring green-up. This habitat mosaic within mature, multilayered coastal rainforests allows deer plasticity during foraging and ameliorates the effects of winter weather on food supplies. The deer on Channel Island spent time in all associations; the habitats they chose determined forage availability and activity costs. The deer recognized and discriminated between associations on the basis of food resources, depending on environmental constraints; the amount of forage available and the choice of diet determined nutrient intake. This flexibility may be particularly important to island populations of deer and coastal populations of animals that cannot seek alternative winter habitats when restricted by steep elevational gradients.

CONCLUSIONS

Our expectations derived from reductionist studies were confirmed. The deer of Channel Island existed in a situation where availability and nutritional quality of forage (especially its digestible energy concentration) dominated all other environmental factors in determining their health, growth, and reproduction. Forage resources were critical year-round, not just during the season of least availability. Particular forage classes (and species) contributed extensively to specific periods of intake.

Some forages were more important than we had anticipated. Skunk cabbage was a major source of energy and protein when it was available. Its large leaf size contributed to very high rates of dry matter intake and foraging efficiency. Although its importance was greatest in spring, when it was among the first species to resume growth, it was avidly eaten throughout the year. Similarly, devil's club leaves (also highly nutritious and large) were eaten throughout seasons of availability and constituted a major food resource. Arboreal lichens also were eaten in much greater quantity than we had anticipated. We had recognized all 3 of those species as important food resources on the basis of their nutritional qualities, but had underestimated their quantitative role in the diet. A fourth very important species was entirely unanticipated: shield fern rhizomes had never been reported as an important forage for black-tailed deer and are seldom considered in assessments of forage availability because they occur below ground. The deer, however, actively sought them during winter when forbs and shrub leaves were in short supply. All of these forage species tend to be underestimated in dietary studies based on rumen or fecal analyses because of their high dry matter digestibilities (Hanley et al. 1985).

Although changes in the body condition and mass of deer on Channel Island during winter were more strongly determined by reduced energy intake than by elevated energy expenditure, snow and cold temperatures also were significant. Increased costs of locomotion when sinking depths in snow exceeded 25 cm made energy expenditure the primary determining factor. Similarly, operative temperatures less than lower critical temperature occurred more often in summer than in winter (as expected), but their magnitude and energy costs actually were greater in winter than in summer. The relative role of energy expenditure, therefore, was very significant during cold, snowy weather, and energy expenditure was relatively more important than we had expected on the basis of other modeling analyses of energy balance (Fancy 1986, Hobbs 1989).

The overall agreement of our observations with predictions is encouraging for the credibility of reductionist studies in nutritional ecology of wild animals. The discrepancies were matters of relative degree of importance. Generally, they were related to the time–activity budgets of the animals, and time–activity budgets are among the most difficult behavior patterns to predict. The time allocated to eating skunk cabbage, for example, is not simply a matter of instantaneous foraging efficiency, which we can predict reasonably accurately. It also is a matter of total diet selection as a function of foraging efficiency (partially), chemical defense and/or detoxification (McArthur et al. 1993), and rumen processing time (Spalinger et al. 1986, 1993), which we cannot predict with nearly as much accuracy. Further, patterns of forage selection and intake change between and within foraging bouts (Gillingham and Bunnell 1989, Gillingham et al. 1997). Similarly, energy costs of locomotion and thermoregulation during periods of winter severity depend on time–activity budgets that are influenced not only by food biomass and macroclimate, but also by the spatial distribution of foods and microclimates (extremely variable and unpredictable). Nutritionally based models of the full complement of environment–animal–behavior interactions, therefore, remain complex.

An understanding of food resources and the nutritional ecology of deer contributes substantially to predictive ecology. Individual processes can be modeled quantitatively and accurately. Relative quantitative comparison of given habitats on the basis of their forage resources (e.g., Hobbs and Swift 1985, Hanley and Rogers 1989) is achievable. More work remains, however, for precise predictions of behavioral patterns. Our results indicate that the mechanistic approach of nutritional ecology does offer the prospect of a predictive science for field ecologists despite its highly reductionist approach.

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APPENDICES

Appendix A. Seasonal changes in digestible protein content (g/g dry matter), calculated as in Hanley et al. (1992), of the plant species commonly consumed by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

	1988		1989							1990				
Forage species	Oct	Dec	Mar	Apr	May	Jun	Aug	Sep	Dec	Mar	Apr	May	Jun	Aug
Forest forbs and ferns														
Cornus canadensis	0.047	0.072	0.047			0.132	0.072	0.083	0.072	0.041			0.116	0.067
Athyrium filix-femina						0.234	0.102	0.106				0.226		0.083
Fiddleheads				0.227							0.224			
Blechnum spicant	0.058			0.032			0.057	0.058	0.056	0.061			0.070	0.077
Coptis asplenifolia	0.063					0.127	0.061	0.065	0.059	0.054			0.077	0.056
Dryopteris dilatata	0.094				0.184		0.078	0.090	0.104			0.203		0.088
Rhizomes	0.076		0.056						0.070	0.055				
Fiddleheads				0.247							0.248			
Gymnocarpium dryopteris					0.201							0.201		
Lysichiton americanum							0.248	0.085[a]				0.334		0.094[a]
Emergent growth (centers)	0.264			0.311		0.258			0.279	0.264				
Maianthemum dilatatum					0.145		0.089	0.084				0.151		0.077
Polypodium vulgare			0.070					0.110	0.110	0.101				0.093
Prenanthes alata					0.155		0.118	0.115				0.213		0.116
Rubus pedatus	0.073				0.168		0.086	0.085	0.080	0.066			0.086	0.094
Streptopus amplexifolius					0.189							0.182		0.086
Streptopus streptopoides					0.155		0.096	0.091				0.161		0.092
Tiarella trifoliata	0.066					0.160	0.084	0.085	0.069	0.056			0.091	0.079
Forest shrubs and trees														
Alnus sinuata						0.113	0.130	0.102[b]					0.145	0.097
Buds			0.078											
Catkins			0.079											
Malus fusca					0.130		0.089	0.000					0.143	0.068
Menziesia ferruginea						0.148	0.075					0.135		0.063
Stems	0.019							0.091						
Oplopanax horridus							0.085	0.066					0.178	0.072
Rubus spectabilis					0.195								0.160	
Sambucus callicarpa						0.184							0.179	
Tsuga heterophylla	−0.001							0.003	0.012[c]	0.009[c]				
Vaccinium alaskaense and *ovalifolium*					0.216		0.094	0.103			0.258			0.092
Stems	0.040		0.045	0.136					0.044	0.059	0.155			
Vaccinium oxycoccus	0.048							0.069						0.056
Vaccinium parvifolium					0.186			0.099				0.194		0.076
Stems	0.044		0.027						0.051	0.036	0.145[d]			

(Continued on following page.)

Appendix A. Continued.

Forage species	1988		1989							1990				
	Oct	Dec	Mar	Apr	May	Jun	Aug	Sep	Dec	Mar	Apr	May	Jun	Aug
Other														
Alectoria and *Usnea* spp.	−0.011		−0.021					−0.020	−0.022	−0.016				
Conocephalum conicum		0.053						0.107						
Lobaria spp.		0.087						0.092		0.104				
Mushrooms	0.135						0.213	0.134						0.168
Peltigera spp.								0.214						
Beach species														
Achillea millefolium								0.101					0.157	0.109
Angelica lucida					0.195			0.103					0.176	
Carex spp.		0.032		0.109		0.062				0.047		0.147	0.092	
Conioselinum pacificum						0.155		0.102					0.179	
Deschampsia caespitosa				0.207										
Elymus arenarius								0.067		0.084				
Equisetum spp.						0.220							0.119	
Fucus furcatus		0.052								0.116				
Glaux maritima													0.070	0.039
Hordeum brachyantherum								0.137						0.120
Ligusticum scoticum						0.229		0.093					0.138	
Plantago macrocarpa						0.082							0.122	
Plantago maritima							0.062	0.099					0.152	0.109
Potentilla egedii					0.147		0.045	0.081					0.139	0.084
Ranuculus occidentalis						0.148		0.125					0.156	0.127

[a] Only midveins of large leaves remaining after foraging by deer.
[b] Deciduous leaves fallen recently to ground.
[c] Seedlings.
[d] Newly emerging buds on stems.

Appendix B. Seasonal changes in digestible energy content (kJ/g dry matter), calculated as in Hanley et al. (1992), of the plant species commonly consumed by black-tailed deer on Channel Island, southeast Alaska, between October 1988 and September 1990.

	1988		1989							1990				
Forage species	Oct	Dec	Mar	Apr	May	Jun	Aug	Sep	Dec	Mar	Apr	May	Jun	Aug
Forest forbs and ferns														
Cornus canadensis	12.02	13.59	12.24			13.48	11.16	11.55	13.59	12.22			13.54	12.36
Athyrium filix-femina						14.80	9.63	10.54				12.64		10.01
Fiddleheads				13.14							13.49			
Blechnum spicant	10.38			10.87			8.83	9.31	12.17	12.32			8.98	9.13
Coptis asplenifolia	13.93					14.10	13.54	12.85	14.75	13.91			14.56	13.79
Dryopteris dilatata	10.60				13.33		9.31	10.24	12.47			12.54		10.66
Rhizomes	10.36		11.24						10.94	12.55				
Fiddleheads				13.09							13.63			
Gymnocarpium dryopteris					12.85							12.53		
Lysichiton americanum							14.80	9.49^{a}				15.46		12.48^{a}
Emergent growth (centers)	14.65			14.71		15.84			15.12	14.89				
Maianthemum dilatatum					14.45		13.61	11.99				14.86		14.01
Polypodium vulgare			11.90					11.81	12.85	13.90				11.15
Prenanthes alata					14.84		13.06	13.08				12.17		13.40
Rubus pedatus	13.42				14.81		13.99	13.26	14.12	14.47			14.41	14.57
Streptopus amplexifolius					16.12							14.11		16.24
Streptopus streptopoides					14.86		13.85	13.16				13.50		14.08
Tiarella trifoliata	11.87					13.47	12.49	11.72	12.37	12.93			13.63	13.64
Forest shrubs and trees														
Alnus sinuata						14.03	13.80	12.03^{b}					13.36	11.78
Buds			12.71											
Catkins			12.50											
Malus fusca					15.23		12.59	15.30					13.56	13.35
Menziesia ferruginea						10.95	10.67					11.00		10.59
Stems	6.42							10.26						
Oplopanax horridus							13.33	13.41					11.76	13.09
Rubus spectabilis					14.44								11.89	
Sambucus callicarpa						14.50							14.95	
Tsuga heterophylla	8.54							8.49	10.72^{c}	12.54^{c}				
Vaccinium alaskaense and *ovalifolium*					16.24		8.09	9.25			12.53			8.33
Stems	7.70		9.55	10.55					9.78	10.48	13.26			
Vaccinium oxycoccus	10.05							9.36						10.16
Vaccinium parvifolium					14.17			11.17				12.64		12.02
Stems	7.53		8.87						10.94	10.88	12.65^{d}			

(Continued on following page.)

Appendix B. Continued.

Forage species	1988		1989							1990				
	Oct	Dec	Mar	Apr	May	Jun	Aug	Sep	Dec	Mar	Apr	May	Jun	Aug
Other														
Alectoria and *Usnea* spp.	12.59		13.67					13.04	13.54	14.49				
Conocephalum conicum		11.00						11.62						
Lobaria spp.		11.43						7.85		14.77				
Mushrooms	13.47						10.38	12.96						13.08
Peltigera spp.								11.36						
Beach species														
Achillea millefolium								12.16					13.11	12.87
Angelica lucida					13.02			11.45					13.58	
Carex spp.		11.30		12.06		12.70				12.06		13.82	10.49	
Conioselinum pacificum						13.53		12.72					13.14	
Deschampsia caespitosa				13.29										
Elymus arenarius								11.35		13.26				
Equisetum spp.						12.25							12.20	
Fucus furcatus		8.64								9.28				
Glaux maritima													13.11	12.87
Hordeum brachyantherum								13.54						12.61
Ligusticum scoticum						10.53		11.28					13.81	
Plantago macrocarpa						11.51							12.38	
Plantago maritima							10.42	11.09					11.35	12.15
Potentilla egedii					13.98		10.49	12.79					13.39	12.72
Ranuculus occidentalis						13.91		13.63					13.41	13.77

[a] Only midveins of large leaves remaining after foraging by deer.
[b] Deciduous leaves fallen recently to ground.
[c] Seedlings.
[d] Newly emerging buds on stems.