

Advances in the nutritional ecology of cervids at different scales¹

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Abstract: Strategies that cervid species use to meet nutritional requirements may vary depending on different spatial and temporal scales. The objective of this review is to provide an overview of contributions made to the field of nutritional ecology over approximately the last 10 y, specifically with respect to cervids. Mechanistic studies using captive animals in confined environments have established cause-and-effect relationships among foraging and digestive efficiencies, food availability and qualities, changes in body mass and condition, and reproduction. Studies using tamed free-ranging cervids in natural habitats have assessed the integrated effects of these reductionist components to validate animal-habitat interactions. At landscape levels, however, wild cervids are not as predictable because behaviours reflect trade-offs between many more variables. Geographic information systems allow for analyses of nutritional values of habitats as broadly indexed by remote sensing imagery, changes in the rates of animal movements (from global positioning satellite-collared animals) in relation to nutritional, energetic, and predation risk factors, and impacts of anthropogenic disturbances. Stable isotopes and fatty acids offer the potential to define spatial and temporal patterns of movements and diets. Further research is needed to determine whether stress hormones and/or nitrogen metabolites are able to provide links with animal condition and population variation. Our challenge is to understand nutritional ecology enough that we can manage for the flexibility in strategies that cervids with different trade-offs on different landscapes use to survive and reproduce.

Keywords: body condition, cervid, energy balance, energy metabolism, forage selection, nutritional ecology, protein balance.

Résumé : Les stratégies utilisées par les cervidés pour répondre à leurs besoins énergétiques peuvent varier selon les échelles spatio-temporelles. Cet article donne une vue d'ensemble des travaux récents (dix dernières années) sur l'écologie de la nutrition, en particulier chez les cervidés. Les études utilisant des animaux en captivité ont montré des relations de cause à effet entre le broutement et l'efficacité de la digestion, la disponibilité et la qualité de la nourriture, les changements de masse corporelle et la condition physique, ainsi qu'au niveau de la reproduction. Les études utilisant des cervidés apprivoisés mais laissés dans leur habitat naturel intègrent toutes ces relations et permettent de mieux comprendre les interactions entre les animaux et leur habitat. À l'échelle du paysage, il est toutefois plus difficile de prévoir les comportements des cervidés sauvages, puisque ces comportements sont le résultat d'un plus grand nombre de variables. Les systèmes d'information géographique permettent d'analyser la valeur nutritive des habitats. À l'aide de la télédétection, on peut aussi étudier les changements qui surviennent dans les déplacements des animaux (grâce aux animaux avec collier émetteur) en réponse à différents facteurs (nutrition, dépense énergétique et risques de prédation) et cerner les impacts des perturbations anthropiques. Pour leur part, les isotopes stables et les acides gras permettent de définir les patrons spatiaux et temporels des déplacements et des régimes alimentaires. Il faudra déterminer, lors de recherches subséquentes, si les hormones de stress ou les métabolites azotés peuvent fournir des indications sur la condition physique des animaux et sur la dynamique des populations. Nous avons maintenant pour défi de comprendre suffisamment l'écologie de l'alimentation pour prendre en considération les différentes stratégies utilisées par les cervidés pour survivre et se reproduire dans divers paysages.

Mots-clés : bilan énergétique, bilan protéique, cervidés, condition physique, écologie de la nutrition, métabolisme énergétique, sélection des aliments.

Nomenclature: Nowak & Paradiso, 1983.

Introduction

Nutritional ecology is the science of relating an animal to its environment through nutritional interactions. Strategies that cervids use to meet nutritional requirements vary according to species and often across different spatial and temporal scales. The objective of this review is to provide an overview of recent contributions to the field of nutritional ecology, with respect to cervids, gained over approximately the last 10 y. In no way is the mention of only recent references meant to minimize the importance of previous studies. I have emphasized mecha-

nistic studies that determine cause and effect relationships at small scales, animal-habitat interactions that test those relationships, and challenges associated with using this knowledge to understand the role of nutritional ecology at large spatial and temporal scales across the landscape.

Small-scale mechanistic studies

ENERGY AND NUTRIENT REQUIREMENTS

Considerable efforts have been made previously to quantify specific energy requirements of cervids to understand the energetic relationships among forage intake, habitat, weather, and energy balance. In the last decade,

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several missing components regarding basal and thermoregulatory costs, reproduction, and field metabolic rates were researched. Pekins, Mautz, and Kantner (1992) conducted a re-evaluation of the basal metabolic cycle in white-tailed deer (*Odocoileus virginianus*). Contrary to the findings of earlier studies (Silver *et al.*, 1969; 1971) that suggested metabolic rates were depressed during winter and served as an adaptation to survival during an energy-limited season, no differences between spring, summer, and winter fasting metabolic rates were observed in more recent studies (Mautz, Kantner & Pekins, 1992). Winter basal rates were similar to prior measurements, but summer rates were lower than previously reported summer values. Mauget, Mauget, and Duncan (1997) also reported no apparent endogenous seasonal rhythms in roe deer (*Capreolus capreolus*). The presumed adaptations in metabolic rhythms reported by previous researchers may have been an artifact of methodological conditions, including differential activity of deer between seasons and previous levels of food intake. More recent studies standardized fasting times, acclimated animals to average seasonal temperatures preceding data collection, and measured metabolism only when animals were bedded. Subsequent measurements by Worden and Pekins (1995) reported that fasting metabolic rates in white-tailed deer may be elevated during fall in response to high levels of intake before metabolic trials and enhanced fat deposition. Work on fallow deer (*Dama dama*; Weber & Thompson, 1998) determined that the seasonal cycles in voluntary food intake were correlated with cycles in mass and body tissues 6-7 weeks later.

Feed intake and its associated heat increment during winter may help substitute for thermoregulation costs and reduce body tissue catabolism by north-temperate cervids (Jensen, Pekins & Holter, 1999). For white-tailed deer on natural browse diets, the increase in thermoneutral heat production resulting from forage intake lowered thermally stressful temperatures by approximately 10°C. Diets with the highest digestible dry matter intake were correlated with the highest heat increments of feeding. Additional studies are needed to define the duration of post-feeding increases in heat production as well as the possible transitory nature of different quality diets (Robbins, 1993). The range of thermally neutral temperatures for different cervid species also depends on age and pelage; most studies have attempted to define lower critical temperatures rather than upper limits to thermoneutrality (Parker & Robbins, 1985). Relative to quantifying the thermal environment of free-ranging animals, regression equations based on air temperatures and wind speeds have been developed for mule deer (Beaver, Olson & Wraith, 1996).

Energy costs throughout the 200-d gestation period in white-tailed deer were measured by Pekins, Smith, and Mautz (1998). More than 90% of the total costs occurred during the last trimester, most of which typically occurs during the onset of spring green-up. Energy costs were 45% greater for pregnant than non-pregnant animals. In northern latitudes where food availability is seasonally restricted, deer that are in the best body condition entering winter are most likely to have adequate body reserves to meet gestation costs during prolonged winters. In roe

deer, increases in resting metabolic rate during gestation were attributed to increasing total body mass of the pregnant female (Mauget, Mauget & Duncan, 1997). Of theoretical interest across cervids would be research to define the relationships between seasonal forage restriction during the gestation period and synchronous breeding, and reproductive flexibility among asynchronous breeders that accommodates varying forage restriction in southern latitudes.

Lactation has been considered to be the most energetically expensive time of year for female cervids. Mauget, Mauget, and Sempere (1997) and Mauget, Mauget, and Duncan (1997) reported energy expenditures by roe deer during the first month of lactation that were 27% above non-lactating animals. This high maternal investment supported elevated metabolic rates and growth rates of neonates; it represents some of the highest maternal reproductive efforts in deer (Mauget, Mauget & Sempere, 1997). Barren-ground caribou (*Rangifer tarandus groenlandicus*), as a medium-sized cervid, mobilize body reserves to meet the demands of producing very concentrated milk for maximum growth rates in a short growing season and actually begin weaning neonates from the first week (Parker *et al.*, 1990). In contrast, roe deer begin weaning after 3 weeks, which is common in cervids (Robbins, 1993; Reese & Robbins, 1994), but their body reserves are small enough (Andersen *et al.*, 2000) that less than half of newborn fawns survive in poor years (Gaillard *et al.*, 1997). Growth rates of woodland caribou (*Rangifer tarandus caribou*) calves were positively correlated with suckling rates during early lactation (Lavigne & Barrette, 1992), but a recent review by Cameron (1998) cautioned that suckling behaviour may not be a consistent predictor of milk transfer to cervid neonates.

Doubly labelled (isotopic) water studies are currently considered to be the most accurate method for directly determining energy expenditures of animals living unrestricted in their natural environments. This technique, however, has been used on only three cervid species (*Rangifer tarandus*, *Odocoileus hemionus sitkensis*, and *Cervus elaphus*; Fancy *et al.*, 1986; Nagy, Sanson & Jacobsen, 1990; Parker *et al.*, 1990; Gotaas *et al.*, 1997; Haggarty *et al.*, 1998; Parker *et al.*, 1999; Gotaas *et al.*, 2000a,b). It is based on the differential losses of labelled hydrogen (^2H or ^3H) and oxygen (^{18}O) via excretion, evaporation, and dilution. An assumption of calculating differences in these rates of loss is that H and O leave the body only as H_2O or CO_2 . Hydrogen, however, may be sequestered in animal fat when animals are gaining mass or lactating (Haggarty *et al.*, 1991), potentially invalidating turnover rates. Further, there may be times of the year when CO_2 is sequestered in growing bones or antlers (affecting the turnover of O) and when increased methane production in response to increased forage intake may remove H from the body pool. Recent studies also indicate significant losses of H in fecal solids (Gotaas *et al.*, 2000a). Without adjustments for these additional losses, results can be variable and sometimes unrealistic (Parker *et al.*, 1999; Haggarty, 2000). Given that estimates of total energy expenditure can be improved by using appropriate adjustment factors (Gotaas *et al.*, 2000a), doubly labelled water provides the only practical way of estimat-

ing energy costs over significant time periods. Data on free-ranging reindeer (*Rangifer tarandus tarandus*) showed large variations between animals of the same sex and age living under identical conditions and energy costs that were much higher than predictions made from captive animals, presumably because of increased locomotory activities (Gotaas *et al.*, 2000b). Additional research should be directed towards determining the applicability of using doubly labelled water during spring and summer, when most known sources of error occur, and to understanding the extent of variation among individuals.

FORAGE SELECTION AND EFFICIENCY

Mechanistic studies have helped advance theories of foraging ecology. Strategies for selection and efficiency appear to be innate, because they do not differ significantly between naïve and experienced animals or between hand-reared and maternal-raised animals (white-tailed deer, Spalinger *et al.*, 1997). Forage selection by cervids is fundamental to understanding ecological relationships because acquisition of food is ultimately related to survival and reproductive output. The nutritional review by Hanley (1997) on the processes of diet selection by deer summarized recent developments in theory and progress towards understanding interactions between deer and their food resource. Although there are interactions between food type and availability, quality of food items has a major influence on the condition of the individual and quantity often determines how many animals survive. Intake is influenced by physiological factors such as age, body composition, and seasonal physiological demands. It is regulated by the time required for rumen passage, which is slower for poor quality forage (Spalinger, Robbins & Hanley, 1993; Spalinger, 1994), and by gut fill, which is highly correlated with body mass (Illius & Gordon, 1992). Body size and its associated mouth size influence general forage types used by deer (Robbins, Spalinger & van Hoven, 1995). Mouth morphology and condition of the mandibular molar teeth play an important role in food processing and the maintenance of body reserves (Kojolo *et al.*, 1998).

Rates of food intake are primarily affected by bite size, which is itself regulated by plant characteristics such as leaf size, geometry, and spinescence (Gross *et al.*, 1993). Intake rates decline with increasing fibrousness of foods, which also affects oral processing rate (Shiple & Spalinger, 1992). The architecture of woody food plants often presents a trade-off between intake rate and food quality (Shiple *et al.*, 1999). Models have been generated to describe the functional response (rates of food intake as a function of food density) by several cervids in dispersed (Spalinger & Hobbs, 1992; Gross *et al.*, 1993) and patchy (Shiple & Spalinger, 1995) distributions of food. Maximum short-term intake rates scale with body mass and correspond closely with scaling of metabolic rates (Shiple *et al.*, 1994). Models of optimal bite size at very fine spatial scales can be used to assess diet quality or plant vulnerability to herbivory by combining both functional responses (involving bite size, fibre concentration, and body mass) and digestive constraints (of body size and gut morphology) (Shiple *et al.*, 1999). They

potentially provide a foundation for understanding plant-animal interactions at larger scales. Gastrocentric models also have been developed to show substantive ingestive and digestive differences among large males, non-reproductive females, and lactating females that potentially explain sexual segregation among cervids (Barboza & Bowyer, 2000; 2001). Differences in feeding activities and niche partitioning between sexes may be driven by digestive function and metabolic demands rather than predation or competitive exclusion. Recent field studies on red deer (*Cervus elaphus*) further indicated that habitat segregation between sexes was driven by net energy gain as indexed by the interaction between foraging opportunities and weather sensitivity (Conradt, Clutton-Brock & Guinness, 2000).

Nutritional value of specific plant species is usually expressed in terms of digestible energy or digestible protein because these are the two nutritional factors most commonly in short supply to deer (Robbins, 1993). Recent studies have addressed the negative influence of plant defensive compounds on these nutritional values, particularly with respect to reductions in digestibility caused by tannins (Hanley *et al.*, 1992). Research by Robbins *et al.* (1991) noted the ability of some species of browsing deer to effectively neutralize the impacts of tannins with tannin-binding salivary proteins. Additional research is needed to address the prevalence of cervid species with such salivary proteins, as well as to define the influence of other non-tannin digestion inhibitors, including terpenes. Research on red deer suggested that tree morphology had a larger influence on feeding behaviour than the content of monoterpenes (Hartley *et al.*, 1997), but black-tailed deer (*Odocoileus hemionus sitkensis*) preferentially selected trees with lower monoterpene defences (Vourc'h *et al.*, 2001). How deer are capable of choosing diets that balance digestible dry-matter intake against digestion-inhibiting compounds relative to chemical defence or detoxification (Tahvanainen, Niemelä & Henttonen, 1991; McArthur *et al.*, 1993) is unknown.

How animals perceive their environment and make foraging decisions is important to our understanding of plant-animal interactions. Foraging behaviour is dependent on spatial distribution of food and non-food items. In environments with prominent seasonal changes, available species, biomass, and bite sizes vary considerably. With changes in forage density and patch size, animals may adjust bite size (Shiple & Spalinger, 1995). Etzenhouser *et al.* (1998) used fractal geometry and tortuosity of foraging paths to show that deer responded to the shape of shrub patches more than to shrub distribution. Both black-tailed and white-tailed deer appear to adjust foraging velocity and movement paths to favour encounters with major food items (Gillingham & Bunnell, 1989; Etzenhouser *et al.*, 1998). Animals of different body sizes travel at similar foraging velocities (Shiple *et al.*, 1996). Use of feeding patches also may be related to specific nutrient intake. Patch use by *Cervus elaphus* was strongly correlated with short-term rates of digestible protein intake (Langvatn & Hanley, 1993), as well as daily rates of energy intake (Wilmshurst & Fryxell, 1995; Wilmshurst, Fryxell & Hudson, 1995). For free-ranging animals, how-

ever, patch and habitat use may be dictated by more than just nutritional factors, including juxtaposition among different patches. Black-tailed deer used winter habitats in proportion to their availability and did not concentrate use in habitats where intake rates of digestible energy or protein were highest; habitat use in summer varied among years in relation to availability or to digestible energy intake (Gillingham, Parker & Hanley, 2001).

Patterns of forage intake are variable and change with preference, selection, and types of food encountered. Gillingham, Parker, and Hanley (1997) reported that black-tailed deer could maintain constant intake rates throughout active periods, could reduce intake rates at the end of bouts, or could increase intake rates towards the end of bouts, emphasizing the need for behavioural observations of complete active bouts. Selection of forage species within the same patch and same foraging bout often changed, as if the search image of the deer completely changed. These selection dynamics argue for distinguishing between available and selected biomass. They also stress the need to consider spatio-temporal variations in trade-offs faced by foraging animals.

The foraging efficiency (rate of energy or nutrient intake in relation to energy expenditure) of cervids provides a critical link between food resources and body condition and performance (Parker *et al.*, 1996). For black-tailed deer in winter, energy intake never exceeded energy expenditure regardless of bout duration, distance travelled, or speed of travel. In summer, metabolizable energy intake rates were four times greater than in winter, and the increased efficiency was associated with mass gains. The ratio of energy intake to requirement is directly related to changes in body mass. Forage resources are critical year-round, not just during the season of least availability. Most emphasis has been placed on the dramatic impacts of winter on energy balance, but it is equally important to recognize the importance of high-quality abundant summer forage to restore body condition and accumulate body reserves. Those reserves are important because nutritional requirements in winter can not be met by foraging alone. As examples, even in mild winters, body reserves met 18-25% of metabolic requirements in black-tailed deer (Parker *et al.*, 1999), 14.2% in caribou (Adamczewski, Hudson & Gates, 1993), and 26% in Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Tyler, 1986). Conversely, from the foraging perspective, even though Svalbard reindeer are known to have large amounts of subcutaneous fat in autumn, approximately 74% of their total energy requirements must be obtained from forage, and most natural mortality is due to starvation in winter (Tyler, 1986).

BODY CONDITION

BODY RESERVES

Many research efforts have been directed in the last decade towards quantifying body condition, because condition is an integration of energy expenditures and food intake, and has direct consequences to reproduction and population dynamics. The probability of conceiving and carrying a fetus to term is determined primarily by summer conditions (and autumn body mass), whereas timing

of parturition and early survival of offspring appears more closely linked to winter nutrition (and effects of early plant emergence on body mass at the end of gestation) (Adamczewski *et al.*, 1987; Bowyer, 1991; Cameron *et al.*, 1993; Langvatn *et al.*, 1996; Ouellet *et al.*, 1997; Hjeljord & Histol, 1999; Post & Klein, 1999). Some adult cervids may be able to compensate for previous periods of moderate undernutrition (Watkins, Hudson & Fargey, 1990; Renecker & Samuel, 1991; Waimiru, Hudson & Price 1994; Eilertsen *et al.*, 2001). In contrast, neonates with low birth weights often are not capable of compensatory growth and therefore, remain among the smallest individuals in their cohort (Parker *et al.*, 1993; Schwartz, Hundertmark & Becker, 1994; Shultz & Johnson, 1995; Pelabon, 1997; Keech *et al.*, 1999) with potentially increased age at first reproduction (Allaye Chan-McLeod, White & Russell, 1995; Adams & Dale, 1998).

Body size and condition of cervids on northern ranges, therefore, are indicators of habitat and weather conditions (Hobbs, 1989) and can be used to predict range shifts and population declines (Ferguson & Messier, 2000). Historically, indices of condition were derived from carcass (or, infrequently, live animal) measurements. They included morphological measures such as chest girth, hind foot length, antler beam, mandible length, body weight, and fetal weight; and organ/gland measures such as adrenal gland size. The morphological measurements typically were considered in addition to fat deposits (*e.g.*, kidney fat, bone marrow fat, and back fat). Recent studies on a variety of cervids continue to use a combination of these indices because body size (body mass or skeletal measurements) and fat reserves affect productivity and recruitment through effects on fecundity and neonatal survival (Case, 1996; Ouellet *et al.*, 1997). Fat, as the major energy reserve in the body, can provide an index of nutritional status and productivity. In moose (*Alces alces*), for example, Heard *et al.* (1997) reported a positive relationship between fertility and fat reserves; Testa and Adams (1998) noted that condition, pregnancy rate, and embryo size were less in females accompanied by young, and Keech *et al.* (2000) showed that females with greater fat reserves gave birth to more twins and produced young with higher birth masses. Sand (1996) observed that moose living in relatively harsh climatic conditions needed a 22% higher body mass to achieve the same probability of twinning as females in mild environments. In caribou, insufficient recovery of body reserves during summer following lactation reduced the probability that females became pregnant (Huot, 1989; Gerhart *et al.*, 1996a); body fat thresholds of 6-7.8% predicted yearling and adult female pregnancy rates (Crête & Huot, 1993; Crête *et al.*, 1993; Ouellet *et al.*, 1997). An increased probability of early embryonic mortality also was linked to low maternal body mass and fat reserves (Russell *et al.*, 1998).

Common post-mortem indices of condition are limited in some of their applications. The kidney fat index is most sensitive for animals in low to moderate condition (*e.g.*, Sika deer [*Cervus nippon*], Takatsuki, 2000), but may be biased by annual and seasonal variations in organ mass that are related to energy expenditure and digestive

efficiency (Gerhart *et al.*, 1996a). Femur marrow fat is a more appropriate index of poor condition. Both indices have limited use for young animals, in which very little fat is deposited regardless of condition and mobilization varies with age, and for which the bone marrow is still very active in red blood cell formation, precluding a colour assessment of condition (Ballard & Whitman, 1987; Saether & Gravem, 1988). Measurements of total body fat can be difficult and expensive data to obtain, but they provide valuable baseline information for understanding and predicting the nutritional condition of wildlife populations. Whole body grinding and chemical extraction to determine mass of major body components (Bois *et al.*, 1997; Cook *et al.*, 2001a; Lesage *et al.*, 2001) are difficult to accomplish in most studies involving free-ranging animals. Consequently, although time-consuming, fat subsamples from different body regions can be used in combination with mass and skeletal measures to predict total body fat in some species (*e.g.*, *Rangifer tarandus granti*; Allaye Chan-McLeod, White & Russell, 1995).

On live animals, condition indices are useful for indicating nutritional status and relating those to life history traits and environmental conditions. Qualitative estimates of condition scoring based on physical appearance or palpation may be limited in precision (Hundertmark & Schwartz, 1998; Cook *et al.*, 2001a,b; Stephenson *et al.*, 2002), but may be useful in assessing condition when body mass determinations are impractical or when actual estimates of fat content are not required (Gerhart *et al.*, 1996b). From a quantitative standpoint, water dilution using hydrogen isotopes (tritium, deuterium) is considered to be the best method to determine body composition. Body fat is inversely proportional to body water content, except in very young animals. From an estimate of total body water, predictions of total body fat can be made from regression equations (Torbit *et al.*, 1985). Because isotope concentrations in blood and urine are similar and related to fecal concentrations, researchers have used urine samples (Parker, DelGiudice & Gillingham, 1993) and fecal samples (Gotaas & Tyler, 1995) to reliably estimate body condition of animals for which blood samples cannot be easily collected. Water dilution has been helpful in quantifying seasonal changes in body composition relative to feed intake and metabolic rate (Worden & Pekins, 1995), differences in the dynamics of body composition between males and females (Schwartz, Hubert & Franzmann, 1988), and the responses to food availability in captive *versus* free-ranging conditions (Parker *et al.*, 1993).

Bioelectrical impedance analysis (BIA), as a more rapid *in vivo* approach to estimating body fat, measures electrical conductivity of the body. Because the conductivity of lipids is 4-5% that of lean body mass, total body conductivity measured across the body between two electrodes can be used to estimate total body fat from regression equations (Robbins, 1993). The technique works most accurately on species that distribute fat relatively evenly over the body (*e.g.*, bears; Farley & Robbins, 1994), but is less useful in ungulates such as caribou (Gerhart, White & Cameron, 1991), elk (*Cervus elaphus nelsoni*; Cook *et al.*, 2001a), and moose (Hundertmark & Schwartz, 2002).

Ultrasonography permits precise determination of rump fat thickness in live animals by scanning the rump region with a portable ultrasound device and measuring fat thickness with electronic calipers. Strong relationships have been developed between rump fat and total body fat for moose (Stephenson *et al.*, 1998), elk (Cook *et al.*, 2001a), deer (Stephenson *et al.*, 2002) and caribou (T. Stephenson, unpubl. data). This index, however, becomes meaningless after rump fat is depleted (< 5.5% body fat in elk; Cook *et al.*, 2001a), although there is potential to measure loin thickness to assess condition in animals without measurable rump fat reserves (Stephenson *et al.*, 2002). Transrectal ultrasonography, scanning the uterine body and both uterine horns, also can be used to detect the presence and number of fetuses in ungulates (Stephenson *et al.*, 1995).

Cook *et al.* (2001b) assessed the applicability of many of the preceding indices to describe nutritional condition in terms of sensitivity, accuracy, and precision. Body condition scoring and ultrasonography were found to be the most reliable indices in elk. From research endeavours to quantify nutritional condition, patterns of fat catabolism have been more precisely defined. The commonly accepted progression of fat being mobilized before protein, first from the rump fat, then subcutaneous reserves, then visceral stores in the omenta and around the heart and kidneys, and finally from bone marrow is simplified and inaccurate. Subcutaneous reserves are not exhausted prior to mobilization of marrow deposits, and mobilization of protein reserves begins before fat stores are depleted (*Odocoileus hemionus*: Parker *et al.*, 1993; Stephenson *et al.*, 2002; *Cervus elaphus*: Cook, 2000; *Rangifer tarandus*: K. L. Parker & P. S. Barboza, unpubl. data).

In contrast to the role of body fat as an energy reserve for survival and reproduction in cervids, which has been well documented (White, 1992), nitrogen (N) requirements for body protein are relatively poorly known. Inadequate N intake results in negative N balance, causing a loss of muscle protein and reduced growth. High reproductive demands for N coincide with periods when forage N is declining or already low, during fall and winter (Parker *et al.*, 1999; Barboza & Bowyer, 2000). For example, rutting males lose significant amounts of body protein (*e.g.*, 25% in *Rangifer*), which is not restored until the following spring when the N content of forage increases with new growth (Barboza & Blake, 1999). Caribou females deposit N in fetuses during winter, and mass of calves at birth is correlated with maternal protein reserves (Adamczewski *et al.*, 1987; Allaye-Chan, 1991). Inadequate N intake for pregnant ungulates compromises maternal tissues (Martin *et al.*, 1997) and reduces fetal viability (Sams *et al.*, 1995), which may ultimately decrease calving rates (Cameron *et al.*, 1993; Russell *et al.*, 1998). Gerhart *et al.* (1996a) noted that protein balance in *Rangifer* could be negative for seven months of the year. Urea recycling and reutilization may help meet the high N demands for fetal growth that coincide with low dietary availability of N. The ratio of digestible energy to nitrogen content of the forage is important because it affects the efficiency of rumen microorganisms (Van Soest, 1994). Greatest uti-

lization of protein in the rumen occurs when a soluble carbohydrate is readily available (Church, 1975). Hence, low-protein forages with high-energy content may help minimize N excretion and spare the use of protein reserves.

Body fat deposits and energy available from spring forage plants seem to support body protein synthesis in the spring (Eilertsen *et al.*, 2001). Lactating females also must allocate protein to milk production (Parker *et al.*, 1990; Allaye Chan-McLeod, White & Holleman, 1994). Strategies for nutrient partitioning indicate, however, that lactating caribou in summer may direct only surplus protein not used to replenish maternal protein reserves towards milk production (Allaye Chan-McLeod, White & Holleman, 1994). Cervid males (and *Rangifer* females) have additional protein requirements for antler growth in spring, although N demands may be lower than previously reported and coincident with abundant forage resources (Asleson, Hellgren & Varner, 1996; 1997).

Isotopic ratios of $^{15}\text{N}/^{14}\text{N}$ reflect exchanges of N between the body and the diet, and between tissues of the body (see reviews in Gannes, O'Brien & Martinez del Rio, 1997; Gannes, Martinez del Rio & Koch, 1998). Animals generally excrete nitrogenous waste enriched in ^{14}N because lighter amine groups (^{14}N) are preferentially removed by enzymes involved in amino acid deamination and transamination. Consequently, urinary nitrogen is lighter than dietary and tissue nitrogen. As the lean body mass declines for animals that are protein-limited, there is an increase in the $^{15}\text{N}/^{14}\text{N}$ ratio because the excreted lighter N is not replaced by dietary protein and tissues become progressively more ^{15}N -enriched. The rate at which tissues become enriched depends on the rate of protein mobilization.

K. L. Parker and P. S. Barboza (unpubl. data) have outlined a conceptual model of body condition in northern cervids that incorporates urinary metabolite concentrations as well as enrichments (δ) of the stable isotope ^{15}N . As N supplies from forage decline between summer and winter, animals may become deficient in N during protein stress (negative N balance), but still have adequate energy supplies (potentially from particular forages or body reserves). A combination of N and energy deficits may occur when body fat is exhausted and forage intake is not sufficient to meet either N or energy demands. Urinary changes associated with a deficit of only N would include altered $\delta^{15}\text{N}$ signatures in urea (because of recycling of nitrogen) compared with creatinine (from the muscle). When both energy and N are limited, increased catabolism of muscle would be associated with increased urinary concentrations of modified amino acids such as 3-methyl-histidine (indicating substantive breakdown of muscle fibres) and hydroxyproline (indicating breakdown of muscle connective tissues). Levels of urinary 3-methyl-histidine have been linked directly to overwinter cumulative mass loss in white-tailed deer (DelGiudice *et al.*, 1998) and to long-term undernutrition in caribou (Case, 1996). Prolonged fasting and deteriorating body condition in deer also are reflected in increased levels of hydroxyproline (DelGiudice, Seal & Mech, 1988). The release of amino-N from body protein would also alter urea kinetics either through an increase in urinary concentration and/or an

increase in circulating blood urea; this change in urea kinetics would alter the $\delta^{15}\text{N}$ in urea. The proposed model is currently being validated on caribou and reindeer as a field-applicable tool for monitoring nutritional condition, including protein reserves, of wintering ungulates (K. L. Parker & P. S. Barboza, unpubl. data).

PHYSIOLOGICAL INDICATORS

Physiological indicators based on components in blood and urine have been used to assess condition of cervids in relation to standard baseline values associated with sex, age, season, pregnancy, lactation, and body weight. Traditional blood serum chemistry profiles (*e.g.*, serum urea nitrogen, albumin, tryglycerides, creatinine, inorganic phosphorus, and alkaline phosphatase) do not typically have significant relations with total body fat (Cook *et al.*, 2001a) or rump fat levels (Keech *et al.*, 1998). Nutrition and insulin-like growth factor-1 (IGF-1) may be correlated (Adam *et al.*, 1995; Webster *et al.*, 1996), but relationships between thyroid hormones (T3, T4) and condition are not conclusive (Watkins *et al.*, 1991; Quinlan-Murphy, 1998; Cook *et al.*, 2001a). The inferred nutritional consequence of high-density populations has no consistent effect on physiological indices (Sams *et al.*, 1998), presumably because of variable responses in dietary protein status, dietary energy status, and protein-energy interactions (Brown *et al.*, 1995).

Urinary samples are used to infer nutritional deprivation and, indirectly, body condition (DelGiudice, Mech & Seal, 1989; Saltz & White, 1991a). Naturally voided urine is often collected as frozen snow; this has the benefit of being a non-invasive sampling procedure with minimal disturbance to the animals (DelGiudice, Mech & Seal, 1988). Changes in urinary metabolites are used to indicate trends in individual condition or population status, although assessments of population condition may be hampered by high variance because of lack of data on age and size of the animals sampled.

Urinary urea nitrogen ratios of creatinine (UN:C ratios) have been the focus of extensive efforts to assess winter nutritional restriction in free-ranging ungulates (DelGiudice, 1995). Use of this index is based on the assumption that with no increase in protein content of the winter diet, an increase in a UN:C ratio occurs only if an animal has depleted most fat reserves and is breaking down endogenous protein at an accelerated rate. The increased rate is reflected in higher levels of excreted urea nitrogen. Creatinine, as a normal breakdown product from metabolic turnover in muscle, is used as a background for UN:C ratios to avoid differences in an animal's hydration state and any dilution effects of the sample in snow (Case, 1994; DelGiudice *et al.*, 1995; 1996; 1997); additional research, however, is needed to quantify the effects of condition deterioration and sub-maintenance diets on creatinine excretion (DelGiudice *et al.*, 2001). In addition to controlled experiments on white-tailed deer (DelGiudice *et al.*, 1987; DelGiudice, Mech & Seal, 1990; 1994), data have been collected on free-ranging populations of deer (*O. virginianus* and *O. hemionus sitchensis*; DelGiudice, Mech & Seal, 1989; Parker, DelGiudice & Gillingham, 1993), elk (DelGiudice, Singer

& Seal, 1991; DelGiudice, Seal & Mech, 1991), moose (DelGiudice, Peterson & Seal, 1991), caribou (Case, 1996; Larter & Nagy, 2000), and Svalbard reindeer (Säkkinen *et al.*, 2001). Limitations of this index have been associated with variation in age/sex classes and with the interpretation of mean chemical ratios from simple random collections of snow-urine samples (Saltz, White & Bartmann, 1995; White *et al.*, 1995b; Säkkinen *et al.*, 2001). Furthermore, elevated urea nitrogen ratios of creatinine may not consistently reflect animal body condition as measured by declining body fat content (Parker, DelGiudice & Gillingham, 1993; Cook *et al.*, 2001a). There may be no physiological basis to estimate body condition from UN:C ratios (DelGiudice *et al.*, 2001) because they reflect the breakdown of lean body tissue rather than the long-term trend in body fat reserves that results from the dynamics of fat depletion, protein catabolism, and energy intake (Parker, DelGiudice & Gillingham, 1993; Case, 1996; White, Garrott & Helsey, 1997). Recent models present a physiological basis for changes in urinary urea nitrogen:creatinine ratios along continuums of body condition and food qualities (Moen & DelGiudice, 1997). Despite the above limitations, there is evidence that average values of this chemical signal may be indicative of relative nutritional restriction at the population level in free-ranging elk (DelGiudice *et al.*, 2001).

Because of direct implications to body condition, allantoin ratios of creatinine recently have been explored as indices of metabolizable energy intake (Garrott *et al.*, 1997). Allantoin is the principal purine derivative in urine in most mammals (averaging 80% in elk; Garrott *et al.*, 1996; Vagnoni *et al.*, 1996). Purine derivatives are products of nucleic acid (DNA and RNA) catabolism. Excretion of purines results from tissue turnover or the digestion of feed and ruminal microbial matter within the small intestine. As the plane of nutrition increases, ruminal growth increases, and urinary purine derivatives increase. The index can potentially be used to show differences between winters or ranges (White *et al.*, 1995b; White, Garrott & Helsey, 1997; Pils, Garrott & Borkowski, 1999). Preliminary analysis of moose urine, however, showed no detectable levels of allantoin, suggesting that uric acid may be the primary purine derivative in moose (Moen *et al.*, 2000) and that allantoin levels may not be a useful index across all cervids. In addition, controlled studies using white-tailed deer noted that increased allantoin:creatinine ratios could result from increasing energy intake, but also could be confounded by accelerated tissue catabolism and increased endogenous contributions to urinary allantoin excretion (DelGiudice *et al.*, 2000).

Glucuronic acid ratios of creatinine also may be an index to dietary quality, because glucuronic acid is a major pathway of excretion of secondary compounds, which generally reduce the nutritional value of forage for cervids. Useful thresholds and the validity of this index as a field tool have yet to be determined (Servello & Schneider, 2000). Potassium ratios of creatinine reflect only very general seasonal differences in food intake (DelGiudice *et al.*, 1987; Parker, DelGiudice & Gillingham, 1993), but they are a poor index of within-season natural

dietary intake (Servello & Schneider, 2000) and show no relation with body condition (Cook *et al.*, 2001a).

Efforts also have been made to monitor stress as an index to condition. Most types of physical and neurogenic stress result in increased secretions of cortisol. Stress may include immediate responses to short-term stimuli and long-term responses to continual disturbance or nutritional deprivation. In terms of long-term winter stress, younger and smaller cervids are more adversely affected than older animals (Saltz & White, 1991a; Parker *et al.*, 1993). Because nutritional stress and body condition are integrally related for free-ranging ungulates during winter, measures of urinary cortisol have been used to assess the energy status of the individual. Cortisol concentrations in snow urine typically reflect levels in pure urine (Saltz & Cook, 1993). Cortisol, as a mobilizer of energy reserves, provides an index to the rate at which an animal's condition is deteriorating (Saltz, White & Bartmann, 1992).

The premise of using cortisol:creatinine ratios to monitor changes in body condition in winter is that cortisol:creatinine levels should increase when the majority of fat reserves have been used during nutritional stress. Animals on high-density ranges have higher cortisol:creatinine ratios than those in low-density areas and cortisol:creatinine ratios increase in animals prior to death (Saltz & White, 1991a,b). Because of the difficulties obtaining urinary or plasma cortisol samples, recent efforts have focused on using fecal cortisol metabolites to evaluate stress responses. New methodologies developed for ten species of mammals (Palme *et al.*, 1998) and specifically for roe deer (Dehnhard *et al.*, 1998) and elk (Millspaugh *et al.*, 2001; 2002) show promise for quantifying metabolic or social stress and anthropogenic disturbances.

Reproductive hormones provide the potential for pregnancy assessment within individuals and populations, as well as broad ecological studies of breeding and synchronized reproduction (Schwartz *et al.*, 1995). During mammalian pregnancy, progesterone and estrogen are produced by the placenta. These reproductive steroids and their metabolites circulate in plasma and are excreted via urine and feces. The ability to distinguish between pregnant and non-pregnant animals using reproductive hormones or their metabolic byproducts varies widely, depending on species, the steroid metabolites measured, the timing of sample collection during gestation, and the antibodies used in the assays (*e.g.*, enzyme immunoassay – EIA [White *et al.*, 1995a] or radioimmunoassay – RIA [Garrott *et al.*, 1998]). Free progesterone (P4) can be quantified routinely in blood, but when metabolized and excreted, is rarely in its original form. It is metabolized to numerous structurally similar steroid molecules (progestagens), which are indirect measures of progesterone in blood circulation. Concentrations of fecal steroids have been measured in caribou (Messier *et al.*, 1990), moose (Monfort, Schwartz & Wasser, 1993; Schwartz *et al.*, 1995), and elk (White *et al.*, 1995a; Garrott *et al.*, 1998). Progesterone and a pregnancy-specific protein B (PSPB) produced by the placenta have been used to indicate pregnancy status from blood sera of various cervids. Progesterone indicates preg-

nancy for mule deer and white-tailed deer (Wood *et al.*, 1986), reindeer, and caribou (Rehlinger *et al.*, 1981; Ringberg & Aakvaag, 1982; Russell *et al.*, 1998). Pregnancy-specific protein B has been found in all ruminants, including mule deer and white-tailed deer (Wood *et al.*, 1986), red deer (Haigh, Cranfield & Sasser, 1988), moose (Haigh *et al.*, 1993; Stephenson *et al.*, 1995), elk (Willard *et al.*, 1994; Noyes *et al.*, 1997; Huang *et al.*, 2000), and caribou (Russell *et al.*, 1998). Progesterone assays appear to be more accurate in detecting early pregnancies in caribou (Russell *et al.*, 1998), whereas levels of PSPB may predict single or twin pregnancies in elk and moose (Huang *et al.*, 2000).

Animal-habitat interactions

Studies using tamed free-ranging cervids in natural habitats have been designed specifically to assess the integrated effects of some of the preceding reductionist components (energy expenditures, forage intake, and the consequences to body condition and reproduction). Intentions of the study designs are to explain wild animal-habitat interactions and to validate whether small-scale mechanistic studies have implications to larger scales. Parker *et al.* (1999) examined the validity of conclusions derived from reductionist studies of nutritional ecology using free-ranging black-tailed deer in a natural forest environment. The results from studies using captive animals to define nutritional and physiological processes provided a strong mechanistic basis for predicting animal-habitat interactions in the wild. In particular, Parker *et al.* (1999) observed that foraging by deer was the predominant activity (92%) within active bouts and that the time spent active varied little throughout the year. Rates of energy and protein intake declined markedly between summer and winter, and although deer showed dietary plasticity in response to forage constraints, they also searched for and specifically selected highly digestible forages (*e.g.*, arboreal lichens) and high-energy bundles (underground fern rhizomes; Gillingham, Parker & Hanley, 2000). Highest intake rates of abundant, high-nutrient, and large bite-sized forages approached the short-term maximums achieved by captive animals (Shipley & Spalinger, 1992; Gillingham, Parker & Hanley, 1997). Supplemental energy costs associated with locomotion in snow were greater than those associated with cold temperatures. In terms of contribution to energy balance, snow affected energy costs to a greater extent than energy intake when snow depths exceeded average carpus height; at low snow depths, however, intake was affected to a greater extent than expenditure because of burial of the herb layer. Deer lost up to 30% of peak pre-winter body mass during mobilization of reserves (Parker *et al.*, 1993). Energy balance appeared to be controlled by energy intake throughout the year, and the availability of digestible energy was assumed to be the primary nutritional factor limiting deer populations in coastal coniferous old-growth forests. This in-depth study of the forage resources used by deer and the relation to metabolic requirements provides a strong basis for prediction of habitat capability for populations of deer (*e.g.*, scaling from the individual animal to the concept of carrying capacity; Hanley &

Rogers, 1989). Further research, though, is needed to determine whether digestible energy content of forages is the primary limiting nutritional factor in other deer-habitat systems, or if the lower protein content of non-coastal forages results in higher rates of protein catabolism than in the black-tailed deer/coastal forest system. Additional efforts should be directed towards the prediction of behavioural patterns of cervids in general, including time-activity budgets that report forage selection in relation to the spatial distribution of foods and microclimates.

In another study designed specifically to assess the integrated effects of nutritionally related factors on animal-habitat interactions, Cook *et al.* (1998) examined the biological connection between thermal cover (which theoretically reduces the rate of net energy loss and negative energy balance) and winter performance in tamed, free-ranging elk. They questioned the fundamental management strategy that vegetative cover enhances survival of wild cervids by conferring energetic benefits that enhance body condition. Their findings indicated that weather-moderating effects were too small, occurred too infrequently, or were too variable to significantly affect body condition. Thermal cover prescriptions actually had negative effects as temperatures declined in winter, in contrast to the positive effects associated with increased solar radiation in open areas. Wind had no measurable effect on elk performance, although windspeeds were usually mild in their study. These results suggest discrepancies between habitat need and preference, and they cast doubt on the paradigm of vegetative thermal value assumed from observations of habitat use. Elk in their study did not attempt to compensate for cover influences by altering activity patterns, even though thermal conditions were severe enough to result in mortalities. Further research may be needed to quantify the effects of acclimation on thermally stressful temperatures, but this study and the modelling efforts of others (Hobbs, 1989) indicate that thermal cover per se is of less importance than other factors (*e.g.*, food intake and total energetic expenditures) to ungulates during winter. More attention should be paid to reassessing habitat effectiveness models, with the inclusion of solar radiation benefits and a greater emphasis on forage abundance and quality, as they relate to the energy intake component of energy balance.

Efforts also are ongoing using field observations of tractable individuals to validate processes of diet selection. Emphases are to quantify trade-offs among patch size and distribution, selected forage biomass, energy costs, and nutrient gain in caribou/lichen systems (W. Collins & D. E. Spalinger, unpubl. data).

Large-scale landscape-level interactions

At landscape levels, wild cervids are even less predictable, because behaviours reflect trade-offs between many more ecological factors. Within large-scale ecosystems, this may include the complexities of multi-prey and multi-predator dynamics (Kunkel & Pletscher, 1999; Ballard *et al.*, 2001; K. L. Parker, B. Milakovic, D. Gustine & A. Walker, unpubl. data). Pastor, Moen, and Cohen *et al.* (1997) reviewed the spatial heterogeneities

associated with animal movements and resource distribution and quality that affect carrying capacities and animal-landscape interactions. These interactions appear to be highly scale-dependent and dynamic. It is imperative, therefore, that wildlife managers and conservation biologists use and refine available techniques and methodologies to indirectly monitor the health of wildlife populations and linkages between species. Geo-graphic information systems (GIS) now allow for data analyses across large areas and provide a means for temporal and spatial extrapolation of data layers related to nutritional ecology.

Large-scale habitat management regimes have largely ignored the effects of nutrition. In the past, inadequate technology has hindered assessments of forage quality and quantity across landscapes by land management agencies (Cook *et al.*, 1998), and there has been a need to develop better techniques to assess forage conditions across the landscape (Cook *et al.*, 1996). Current state-of-the-art techniques, when combined with available survey information, however, will broaden our understanding of ecosystem dynamics.

REMOTE SENSING AND SATELLITE IMAGERY: HABITAT ASSESSMENT

Because of the complexity of large ecosystems, habitat monitoring will likely need to be based on indirect indices. It is unlikely that landscapes will be systematically mapped using ground inventories. Instead, efforts involving satellite imagery can correlate spectral signatures with vegetative-topographic communities that are associated with wildlife value. Space-borne sensors now allow researchers to identify large-scale patterns in ecological systems and to measure large-scale processes as they take place (Roughgarden, Running & Matson, 1991). For example, satellite imagery, often in combination with digital elevation models, has been used to accurately classify vegetative cover types within large geographic areas used by caribou (Johnson, 2000; Griffith *et al.*, 2002) and to conduct rangeland inventory of lichen pastures for reindeer (Colpaert, Kumpula & Nieminen, 1995). Efforts are continuing to classify vegetation communities based on species composition, vegetation density, and vegetation form, vigour, and structure (Markon, Fleming & Binnian, 1995; R. J. Lay, unpubl. data).

Several change detection procedures are available to monitor changes in vegetation greenness. For example, the Normalized Difference Vegetation Index (NDVI) indexes the disproportionate reflectance of near-infrared radiation from green vegetation (Tucker & Sellers, 1986). Because correlations are good between NDVI and primary productivity, NDVI is an index to total green biomass and can be used to assess timing of forage emergence and senescence in a variety of different ecosystems. For example, parturient females of the Porcupine caribou herd in Alaska selected annual calving grounds with a proportionately higher rate of greening (NDVI rate) and areas within the calving grounds with proportionately greater forage biomass (NDVI) and quality (NDVI rate) during calving and peak lactation (Griffith *et al.*, 2002). These data indicate a variable functional response to forage across the landscape, as measured by NDVI estimates.

STABLE ISOTOPE AND FATTY ACID ECOLOGY: FOOD WEB DYNAMICS

Spatial and temporal changes in food selection and animal condition cannot be determined from surveys of animal numbers at very large scales. Further, it is not logistically or fiscally possible to repeatedly inventory animal numbers directly over large areas. Powerful techniques that are associated with stable isotopes (primarily carbon, nitrogen, oxygen, and hydrogen) have been used by plant ecologists and are now being employed by wildlife scientists to help define linkages in food webs and monitor environmental conditions and anthropogenic disturbances (Rundel, Ehleringer & Nagy, 1988).

Stable isotopes function as natural markers to provide insights into diets, particularly in defining geographic, temporal, and age-specific variation in diets. They also are used to infer location histories of highly mobile animals. Species moving between isotopically distinct foraging areas carry with them information on the location of previous feeding. Analyses of carbon isotopes (^{13}C / ^{12}C) can indicate the relative contributions to an animal's carbon pool of C3 and C4 plants or the relative contributions of marine and terrestrial sources (Tieszen *et al.*, 1983). Analyses of nitrogen isotopes (^{15}N / ^{14}N) are useful in determining the trophic position of animals. Because the lighter isotope (^{14}N) is preferentially excreted and because there is a greater net incorporation of the heavier isotope (^{15}N) into the tissues of the consumer, nitrogen-isotope ratios usually increase with each trophic level (see review in Kelly, 2000). Oxygen-18 (^{18}O) can be used to characterize foraging zones and habitat preferences (Clementz & Koch, 2001); deuterium (^2H) shows a North-American-continent-wide pattern in enrichment gradient (Hobson & Wassenaar, 1997).

The turnover rate of isotopes in tissue depends on the tissue's metabolic rate, and, therefore, different tissues provide different dietary information reflecting different time scales. Blood typically has a higher turnover rate than muscle, which is more metabolically active than bone (Hobson & Clark, 1993; Hildebrand *et al.*, 1996). Constituents within whole blood also have different turnover rates: red blood cells reflect metabolic events that occurred within the last 3-4 months, whereas plasma proteins are more responsive to changes in the previous week. Hooves represent a sink for carbon and nitrogen and, therefore, have the potential to represent seasonal oscillations (Kielland, 2001).

Most research using stable isotopes has been directed towards quantifying diets of seabirds, marine mammals, and terrestrial carnivores. Relatively few studies have involved cervids, largely because herbivores consume foods that have high variability in nitrogen concentration and they employ processes such as urea recycling that can alter assimilation of different isotopes. Stable isotopes, however, can differentiate generally between grazers and browsers and between species that feed on the forest floor, in the forest canopy, or in the savanna grasslands of Africa (Ambrose & DeNiro, 1986). Variation in hoof and antler tissue of reindeer and moose that encounter very different foraging environments in summer and win-

ter indicates seasonal switching between graminoid/forb-based diets and shrub-based diets (Barnett, 1995; Kielland & Finstad, 2000; Kielland, 2001), although nutrient recycling may confound interpretations (Ben-David, Shochat & Adams, 2001).

Stable isotope analyses also provide a link between ecosystem processes and behaviour of predators (Ben-David, Shochat & Adams, 2001). Stable isotopes can identify the relative importance of herbivores *versus* vegetative matter in the diets of carnivores (Hobson, McLellan & Woods, 2000). They also can potentially distinguish between prey species in carnivore diets based on distinct signatures among prey (Ben-David, Flynn & Schell, 1997; Ben-David, Shochat & Adams, 2001). In addition, if isotopic differences between adults and young are established (as determined for caribou), the proportion of newborn and adult prey in predator diets can be estimated (Jenkins *et al.*, 2001). Recent advances in the development of multiple-source and concentration-weighted mixing models (Ben-David, Flynn & Schell, 1997; Phillips & Koch, 2002) improve our abilities to quantify the contribution of cervids to predator diets and define the extent of prey switching among species (Szepanski, Ben-David & Van Ballenberghe, 1999).

Methods of fatty acid signature analysis are still being developed, but already have been used to identify the general trophic level of diets and to detect major and minor shifts in diet within populations (Iverson, Arnould & Boyd, 1997). The use of fatty acids in studies of foraging ecology is based on the premise that long chain fatty acids (with carbon chain length 14 or greater) are deposited in animal tissues with minimal modification from the diet. Because of specificities in the biosynthesis and modification of fatty acids among different species, many components appear in animal tissues that have a specific ecological origin (Iverson, Arnould & Boyd, 1997). Unlike proteins and carbohydrates that are broken down during digestion, dietary fatty acids in monogastric animals pass directly into circulation intact. In non-simple-stomached cervids the fatty acids do not always remain intact, but may be altered by bacterial metabolism, and interpretation is more complex. Nonetheless, depot fat composition is related to feeding type: concentrate-selective feeders, grass and roughage eaters, and intermediate mixed feeders (Meyer *et al.*, 1998). Current efforts are being made to determine whether fatty acid signatures from northern ungulates (caribou and moose) are different enough that components in the diets of their predators (bears and wolves) can be quantified (S. D. Farley, unpubl. data).

GLOBAL POSITIONING SATELLITE LOCATIONS: DEFINING SCALES OF MOVEMENT

Global positioning satellite (GPS) collars that allow frequent successive relocation data can be used to identify animal-defined spatiotemporal scales of movement and, in combination with remote sensing, identify flexibility in the strategies that animals use for resource selection. Recent studies by Johnson, Parker, and Heard (2001) and Johnson *et al.* (2002a) used the breakpoint in frequency of movement rates to define large- and small-scale movements across the landscape. During small-scale move-

ments, which were assumed to be representative of foraging bouts, predation risk had little influence on the selection of specific cover types by caribou (Johnson *et al.*, 2002b). At feeding sites, animals did not select those species with the highest digestible energy or protein content, but rather areas where available biomass was greatest (Johnson, Parker & Heard, 2000; Johnson, Parker & Heard, 2001). This may reflect that lichen species with the highest digestible energy were not necessarily the most easily handled, resulting in lower short-term profitability (Fryxell, 1991). Large-scale inter-patch movements by caribou occurred in habitats with lower energetic costs of movement and often greater risks of predation (Johnson *et al.*, 2002b). Bergman, Schaefer, and Lutich (2000) modelled seasonal and annual movements of both migratory and sedentary caribou at even larger temporal and spatial scales. Data from all of these studies suggest that cervids respond to the environment hierarchically. In heterogeneous landscapes, this involves trade-offs between predation risk, energetic costs of movement, and vegetative characteristics, and the complexity of foraging choices increases when animals attempt to minimize risk while meeting nutritional requirements (Heard, Williams & Melton, 1996; Kie, 1999). Conservation strategies should identify the scale-dependent factors that drive the dynamics of cervid populations.

CLIMATIC REGIMES: IMPLICATIONS TO CERVIDS

Climatic variability across large scales and the implications of global warming are a challenge to modellers and managers. Climatic regimes influence life history patterns by altering size-fecundity thresholds. Moose, for example, do not mature or attain a specific fecundity at a fixed size or age (Sand, 1996); rather, reproductive strategies are affected by the combination of winter harshness and summer nutritional conditions. Winter severity at relatively small scales and its interaction with body mass dynamics previously received considerable attention by researchers, particularly relative to the ability of neonates to survive the first winter (Cederlund, Sand & Pehrson, 1991). Over large areas, some studies of recruitment have determined that winter harshness has no consistent effects on calf survival (moose, roe deer, and red deer: Loison & Langvatn, 1998). Others have shown that winter harshness during the first winter is a key factor in the lifespan of cervids at northernmost parts of their ranges (red deer: Loison & Langvatn, 1998; white-tailed deer: Lesage *et al.*, 2001). Increasing winter severity may also increase implantation failure in roe deer (Hewison & Gaillard, 2001).

Climatic variation at landscape scales is likely to influence population dynamics of cervids through changes in nutrient quality at foraging areas. Plant digestibility during summer has been assumed to increase with latitude and colder climates (Albon & Langvatn, 1992; Sand, 1996). Lenart *et al.* (2002), however, reported that increased cloudiness or shading during summer reduced biomass, increased N content, and often decreased dry matter digestibility. The potential impacts of climatic changes on physical condition and reproduction are further influenced by population size and vulnerability to predators (Bowyer, Van Ballenberghe & Kie, 1998;

Barten, Bowyer & Jenkins, 2001; Patterson & Power, 2002; Kie, Bowyer & Stewart, 2003). Future predictions related to wildlife species will likely benefit from many of the preceding landscape-level techniques.

Conclusion

In this review, I have provided a very broad overview of the contributions to the field of nutritional ecology of cervids over approximately the last 10 y. Periods of nutritional stress typically characterize free-ranging cervid populations. Most studies have been directed towards northern regions where nutritional restriction occurs during winter. Less attention has been given to cervids that are nutritionally stressed during hot, dry summers. Studies also have focused on north-temperate species, with most research conducted on white-tailed deer, roe deer, and *Rangifer*.

Small-scale mechanistic studies have defined cause and effect relationships usually by using captive animals for physiological and nutritional projects. These studies provide a quantification of what cervids are physiologically capable of doing and give some indication as to why they use their environments as they do. Very few studies with free-ranging animals have assessed the integrated effects of reductionist components related to nutritional ecology. There are, however, animal-habitat observations that confirm general predictions from controlled studies even when animals use different strategies to meet nutritional requirements. At the landscape level, wild cervids are less predictable because behaviours reflect trade-offs between many more variables. New technological tools, however, offer the opportunity to apply our nutritional understanding to landscape-level questions that address environmental and anthropogenic changes. We have the potential to quantify habitats and changes in nutritional value across the landscape using remote sensing imagery, to quantify interactions among predators and prey using stable isotope ecology, and to quantify movements and use of the landscape by cervids with GPS telemetry. Our major limitation at this time is a sound index to animal condition. If urinary or fecal metabolites could be used reliably to indicate changes in nutritional status, wildlife managers would have additional information on body condition and implications to neonatal recruitment. This information would contribute to a better understanding of what changes in landscape conditions may be of potential concern relative to anthropogenic disturbances (*e.g.*, displacement from natural habitats) or climatological change (*i.e.*, global warming). Concentrating future efforts on large-scale interactions will help define the flexibility in life history strategies that wild cervids use to survive on different landscapes.

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