Are nutritional limitations in northern ungulates paradoxical?

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Abstract: Nutritional paradoxes are conclusions about nutrition that seem counterintuitive or self-contradictory at first, but upon deeper investigation turn out to be well supported. We summarize 6 scenarios for northern ungulates (i.e., bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), caribou and reindeer (*Rangifer tarandus*), elk (*Cervus elaphus*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), mule deer and black-tailed deer (*Odocoileus hemionus*), muskoxen (*Ovibos moschatus*), thinhorn sheep (*Ovis dalli*), and white-tailed deer (*Odocoileus virginianus*) in which a nutritional limitation seems paradoxical, including imbalanced diets, forage nutrient density, phenological mismatches, abundant vegetation (Green World), high pregnancy rates, and population persistence. We deconstruct each perceived paradox, reducing it to its basic assumptions, and illustrate how evolved physiology, behavior, and life-history traits allow northern ungulates to persist in their environments, even when nutrition is limiting, thus resolving the paradoxes. We provide suggestions for study designs to avoid common pitfalls and misconceptions associated with each paradox that can otherwise perpetuate perceived paradoxes and jeopardize ungulate management and conservation. Even when nutritional limitations occur, they do not preclude the influence of other factors in limiting or regulating populations; rather nutritional limitations may exacerbate the effects of other factors, making it even more important to understand the role of nutrition. Failing to recognize the role of nutrition in the ecology of northern ungulates can lead to erroneous conclusions that result in conservation and management actions that are ineffective or counterproductive. A strong foundational knowledge of nutritional ecology and associated adaptations of ungulates can help ensure nutritional limitations are not overlooked.

Key words: Body fat, forage maturation hypothesis, forage quality, functional response, Green World Hypothesis, match-mismatch, trophic mismatch.

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Introduction

Nutritional paradoxes are conclusions about nutrition that seem self-contradictory at first, but upon deeper investigation, are well supported. Often, nutritional paradoxes are semantic paradoxes, in that they involve faulty assumptions or ideas, rather than logic paradoxes (Ramsey, 1926). For example, summer nutrition frequently is limiting for northern ungulates (Crête & Huot, 1993; Cook et al., 2013; Hurley et al., 2014; Smiley et al., 2022), which may seem counterintuitive because summer is the time of year when forage quantity and quality peak (Parker et al., 1999, 2009). During summer, however, nutritional requirements are elevated to support lactation, calf growth, and accretion of body reserves, which are important for overwinter survival and population growth (Post & Klein 1999; Cook et al., 2004; Albon et al., 2017; Denryter et al., 2022a). In many cases, however, forage quality or quantity may not be adequate to support food intake rates needed to meet requirements during

summer (White et al., 1975; Cook et al., 2016; Denryter, 2017; DeYoung et al., 2019). Thus, animals coming off summer range in poor nutritional condition may face heightened risk of mortality over winter (Denryter et al., 2022a; LaSharr et al., 2023a), which, along with decreases in body condition over winter, can result in the conclusion that winter is the greatest nutritional bottleneck of the year (Klein 1965; Hobbs et al., 1982; Torbit et al., 1985). That conclusion, however, ignores potential issues with forage quality and quantity during summer and the importance of seasonal carryover effects that influence individual productivity and survival (Cook et al., 2013; Hurley et al., 2014). Recognizing that nutritional limitations can occur during summer has helped highlight the importance of summer habitats in the conservation of northern ungulates (Russell et al., 2021; Denryter et al., 2022b).

Nutritional paradoxes can be perplexing because they challenge common assumptions or obvious conclusions and may even violate biological laws. For example, Gause's Law, or the competitive exclusion principle, states that two species that compete for the same resource cannot coexist at constant population values; one species will be outcompeted by the other and go extinct or it will evolve to fill a different ecological niche. Competitive exclusion rarely occurs in natural systems, however, because species exploit heterogeneity in resources (Roy & Chattopadhyay, 2007). The paradox of the plankton (Hutchinson, 1961) is a classic example that violates the competitive exclusion principle—despite limited resources, many species of plankton coexist without being driven to extinction or evolving to fill a new niche. In terrestrial systems, cervids violate Bergmann's Rule (Bergmann, 1847), which states that body size increases inversely with temperature such that intraspecific body size should increase with latitude. Cervid body size, however, is better described by duration of the annual productivity pulse than by temperature (Geist, 1987, 1990), and selection for smaller body size at northern latitudes, such as the gradient in body size of caribou (Rangifer tarandus spp.), is the result of nutritional stress (Klein et al., 1987; Couturier et al., 2010). These examples illustrate how well-established phenomena can seem paradoxical yet are explained through the lens of nutritional ecology.

From an applied perspective, nutritional paradoxes may have important consequences for management and conservation, especially if they mask the role of nutrition in the ecology of northern ungulates. For example, assuming winter is the predominant season of nutritional limitation because animals usually lose fat over winter ignores the adaptive value of fat loss (Tyler *et al.*, 2020) and oversimplifies more complex aspects of nutritional ecology, such as state-dependent and risk-sensitive changes in body fat, including fat gains overwinter (e.g., Monteith *et al.*, 2013; Denryter & Crouse, 2025). Thus, the primary aim of our review was to illustrate how nutritional paradoxes can mask the role of nutrition in the ecology of northern ungulates. We deconstruct perceived nutritional paradoxes to their basic assumptions and describe how these paradoxes can be resolved by a deeper understanding of evolved animal physiology, behavior, and other life-history traits. We focus on northern ungulates because the role of nutrition sometimes has been underappreciated or misunderstood, owing to insufficient data and methodological limitations (Brown *et al.*, 2007), particularly when there is assumed to be an abundance of available food, limitations are thought to be strictly density-dependent, or because pregnancy rates are high (Festa-Bianchet *et al.*, 2011). We provide suggestions for study designs to avoid common pitfalls and misconceptions associated with each paradox. Our examples focus largely on ways that nutrition can be limiting regardless of animal density, although density-de-

pendent nutritional limitations are important and well-documented (Skogland, 1983; Stewart *et al.*, 2005; McCullough, 2006; Bowyer *et al.*, 2014). Throughout our review, we use the term *nutritional limitation* to refer to any reduction in animal performance (e.g., mass and fat gain in summer) or population productivity (e.g., reproductive output and recruitment) in relation to the maximum biological potential on a plane of nutrition that meets or exceeds requirements.

The Imbalanced Diet Paradox

Animals require organic macronutrients (i.e., carbohydrates, fats, proteins) and inorganic minerals (e.g., phosphorus, sodium, magnesium, selenium, and cobalt) in their diets. Macronutrients make up most body tissue and serve many physiological functions (e.g., enzymes, carrier molecules, energy metabolism, hormone production), whereas minerals serve a variety of biochemical and structural roles (e.g., scavenging free radicals, maintaining electrochemical gradients, matrix structure of bones and teeth, immune function; Robbins, 1993; Suttle, 2010). Forages provide carbohydrates and protein but often are low in fat and minerals (Staaland & White, 2001; Robbins, 1993). Yet ruminants can accrete large fat reserves (e.g., >20% of body mass; Denryter *et al.* 2022a) and true mineral deficiencies that result in constraints to physiological and productive processes in free-ranging ungulates are uncommon (but see Flueck, 1994). The basic assumption of the Imbalanced Diet Paradox is that northern ungulates, most of which are ruminants, must acquire fat and minerals from forages in their diets to satisfy nutritional requirements.

To meet the demands of living on a plant-based diet that is low in fat, ruminants have co-evolved with microorganisms that adhere to plant fibers in the rumen and release enzymes capable of digesting fibers, including cellulose, into their component parts (sugar molecules). Microorganisms ferment sugars to produce volatile fatty acids (VFAs), which are the primary source of energy for ruminants. Among VFAs, acetic acid (acetate) occurs in the highest concentration and reacts with Coenzyme A to become acetyl-CoA, which is a substrate for fatty acid synthesis (Ungerfeld, 2020). Fatty acids produced from acetyl-CoA are metabolized into triglycerides, which are a precursor of body fat. Some amino acids (from proteins) and fatty acids in plants also can be used to produce fat via biochemical pathways of intermediary metabolism (e.g., Tricarboxylic Acid Cycle; Folley & French, 1950) (Fig. 1). Given the biochemical pathways of lipogenesis, ruminants have evolved to require only ~1–3% of their dry matter intake as essential fatty acids (Robbins, 1993; Smith, 2023). Ruminant evolution is so attuned to a low-fat diet that high-fat diets can be disadvantageous because high dietary fat can inhibit fiber digestion and decrease dietary digestibility (Ikwuegbu & Sutton, 1982; Jenkins & Palmquist 1984). During summer-autumn, northern ungulates can shunt excess VFAs, including acetate and butyrate, to fat accretion (Larsen *et al.*, 1985). Large fat stores facilitate earlier breeding and birth dates, greater birth mass, greater neonate survival, as well as greater overwinter survival of adults, and can provide resources for milk production particularly in early lactation (Oftedal, 2000; Cook *et al.*, 2004; Monteith *et al.*, 2014).

Rarity in mineral deficiencies for northern ungulates is due in part to numerous physiological adaptations that allow them to survive on diets with low concentrations of minerals. As with fat and protein, northern ungulates can accrete body stores of minerals that allow ungulates to tolerate seasonal declines in mineral availability (Care *et al.*, 1979; Staaland & Sæbø, 1993). To maintain normal physiological functions for antler and bone growth and muscle contraction when sodium, phosphorus,

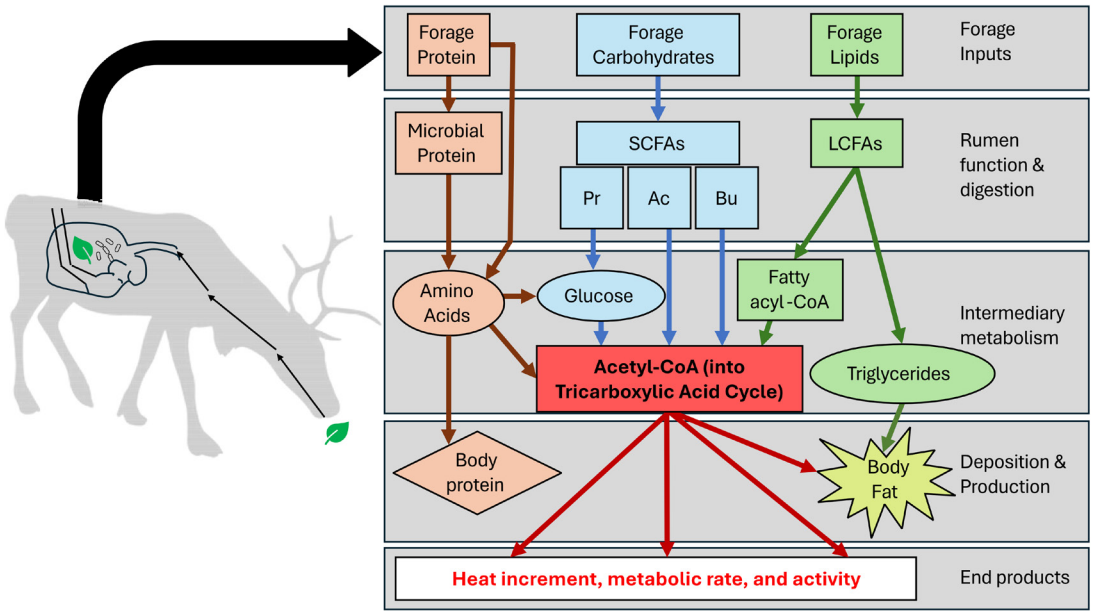

Figure 1. Forages are transmitted from the mouth, via the esophagus, to the rumen, where they are fermented (carbohydrates and proteins) or hydrolyzed (lipids) by a diverse microbial community. Microbes provide most protein to the ruminant. Microbial protein, plus dietary protein, provide amino acids for body protein, glucose, and acetyl-CoA. Short-chain fatty acids (SCFAs; propionate (Pr), acetate (Ac), and butyrate (Bu)) produced via fermentation provide glucose and Acetyl-CoA. Long-chain fatty acids (LCFAs) are converted to fatty acyl-CoA and then acetyl-CoA or triglycerides. Acetyl-CoA is routed through the tricarboxylic acid cycle for energy metabolism and through intermediary metabolism to yield LCFAs that are esterified to triglyceride and deposited as body fat (intermediary metabolism steps are not illustrated in the figure).

and calcium are deficient, northern ungulates modify metabolism and maintain activity of various enzymes in serum, such as alkaline phosphatase and calcium-regulating proteins (Staaland *et al.*, 1980; Grasman & Hellgren, 1993; Moen & Pastor, 1998; Mänttäri *et al.*, 2013). Some enzymes involved in mineral metabolism, such as glutathione peroxidase, also have higher activity in wild than domestic ruminants, which reduces mineral requirements of wild ruminants (Robbins *et al.*, 1985). Minerals such as sodium are conserved through physiological adaptations in the kidneys, including a large resorptive capacity (Weeks & Kirkpatrick, 1976; Belovsky & Jordan, 1981) and preferential retention (Cameron, 1972), as well as through hindgut absorption (White *et al.*, 1984; Holand & Staaland, 1995).

Selective foraging, in which animals consume specific plants or plant parts more than expected based on availability (Ivlev, 1961), is also an important adaptation that helps resolve the Imbalanced Diet Paradox. Selective foraging is in part underpinned by nutritional wisdom, which is the animals' innate or experientially learned ability to make dietary choices based on nutritional needs (Provenza, 2006). During autumn, which is an important time of year for fat accretion in northern ungulates, white-tailed deer (*Odocoileus virginianus*) selectively forage acorns in some areas (Harlow *et al.*, 1975), even increasing home range size to seek acorns (McShea & Schwede, 1993). When acorns are not available, deer experience

a 40% reduction in energy intake (Mautz & Pekins, 1988). Acorns are not available to all northern ungulates, which instead select other forages associated with a high VFA production rate (White & Staaland, 1983). Similarly, moose (*Alces alces*) and reindeer (*Rangifer tarandus*) selectively forage aquatic plants to acquire sodium and potassium (Belovsky & Jordan, 1981; Fraser *et al.*, 1984; Staaland & Sæbø, 1993; Ohlson & Staaland, 2001). Selective foraging allows ungulates to balance competing needs for macronutrients and micronutrients (Kubota *et al.*, 1970; Felton *et al.*, 2021).

In addition to selective foraging, behavioral adaptations to low-mineral diets of northern ungulates include geophagy (soil consumption) and migration. Geophagy is perhaps the most common behavioral adaptation in northern ungulates to avoid mineral deficiencies on a plant-based diet (Hebert & Cowan, 1971; Heimer, 1974; Tankersley & Gasaway, 1983; Arthur & Gates, 1988; Klein & Thing, 1989; Ayotte *et al.*, 2008). Patterns of geophagy vary seasonally in relation to need (Fraser *et al.*, 1984; Staaland & Hove, 2000; Rea *et al.*, 2013). Seasonal movements also help mitigate mineral deficiencies by providing access to mineral licks or forages replete with sodium or other minerals (Staaland & White 2001; Ayotte *et al.*, 2008; Oster *et al.*, 2018: Enns, 2021).

Studies aiming to understand more about the role of fat in the diet of ungulates could measure digestible energy of forages to provide some insights into the potential for fat accretion, especially as it can be related to nutritional requirements, intake, and overall energy balance. Additionally, studies that allow researchers to predict potential VFA production of forages may provide insights into which forages are most important for fat accretion and how that influences forage selection. Studies aiming to evaluate the potential for free-ranging ungulates to be limited by minerals are difficult to accomplish. Mineral requirements are poorly understood for northern ungulates and blood or hair samples are generally not precise indicators of mineral nutrition (Combs, 1987; Herdt & Hoff, 2011). Studies relying solely on plant samples provide inadequate information for evaluating potential mineral limitations if animals have access to licks and mineralized water sources. Longitudinal datasets that track individuals and their mineral levels and relate these to individual performance and productivity over time, or in the context of the overall population (increasing, decreasing, stable) and other limiting factors, will provide more definitive information about mineral nutrition.

The Forage-Nutrient Density Paradox

Forage quality often is evaluated by determining how concentrations of nutrients (e.g., kJ energy/g of food or g protein/100 g of food) in individual food items or diets compare to nutritional requirements for those nutrients in the species of interest. Forages that provide concentrations of nutrients that are greater than or equal to requirements are considered adequate to meet requirements (i.e., can support animals), whereas forages providing nutrient concentrations that are less than requirements are considered inadequate to meet requirements (i.e., cannot support animals). Recent work on caribou demonstrated that at the scale of dietary (forage) nutrient density, digestible energy and digestible protein often were below requirements for lactation, but protein was more limiting (Denryter *et al.*, 2022b). The same study, however, showed at the scale of daily intake, energy was far more limiting than protein. These findings suggested a paradox in that protein could be limiting at the diet scale but not at the scale of daily intake, even though daily intake is a function of dietary forage nutrient density.

The basic assumption of the Forage-Nutrient Density Paradox is that ruminants are limited by forage digestibility and nutrient (energy or

protein) concentrations that are below levels necessary to meet requirements, but it is important to understand how those requirements are estimated. There are two basic methods to estimate nutritional requirements of ruminants as a nutrient density. Empirical studies estimate required nutrient concentrations in the diet for a given level of performance (e.g., mass gain, fat gain, growth), with treatment groups having *ad libitum* (free access) to feeds of varying levels of quality (e.g., Cook *et al.*, 2004); such studies are rare for wildlife. Alternatively, requirements can be modeled based on assumptions about metabolic rates, how fast animals eat (i.e., intake rates), and how long animals spend eating (i.e., foraging time). For example, to estimate dietary digestible energy requirements, we would divide the daily requirement for digestible energy (determined from basal metabolic rates and other energy expenditures) by the animal's total daily intake of food. That approach gives a single value for digestible energy requirements but does not allow for any flexibility by animals in diet selection, intake rates, or foraging time. If ungulates can increase any of those factors, the concentration of nutrients required in the diet decreases. An important caveat is that increasing foraging time and per-minute intake rates are only possible when diet quality is greater than ~12.6 kJ/g (~3.0 kcal/g) of digestible energy or ~70% dry matter digestibility because of physiological constraints that set limits on intake below those values (Minson & Wilson, 1994; Van Soest, 1994; Cook *et al.*, 2004).

There are other hypothetical situations in which northern ungulates could meet daily requirements when dietary concentrations are "below requirements" or fail to meet daily requirements when dietary concentrations are "above requirements". If ruminants select diets wisely, they can include individual items that are below requirements for a given nutrient and still meet requirements as long as the overall diet averages at or above requirements (Hanley *et al.*, 2012). During winter, generally most forages are "below requirements", but northern ungulates have adapted to minimize energy requirements via reduced activity, nocturnal hypometabolism (Arnold *et al.*, 2003, 2018), and mobilization of body stores to offset poor forage quality and limited forage availability during winter (Mautz, 1978; Tyler & Blix, 1990; Monteith *et al.*, 2013; LaSharr *et al.*, 2023b). Nonetheless northern ungulates may fail to meet requirements despite adequate dietary concentrations of nutrients when quantities of food are sparse and cannot be consumed rapidly enough to meet requirements or they fail to store adequate reserves to offset seasonal deficiencies.

Studies aiming to evaluate the potential for free-ranging ungulates to be limited by nutrient density of forages are difficult to accomplish unless digestibility constraints and requirements for forage digestibility and nutrient composition are known. Recent efforts to model requirements have been accomplished for many northern ungulates (Denryter & White, *In press*), but few of these have been estimated empirically. Additional studies to estimate forage digestibility and nutrient density requirements for northern ungulates are needed. In the meantime, studies to evaluate potential limitations should proceed cautiously and disclose uncertainty about estimated requirements and physical capabilities of animals. If available, tame animals can be used in field settings to provide insights into what a species is physically capable of and avoid assumptions about what animals *might* be able to do at different levels of forage digestibility and nutrient density (e.g., Trudell & White, 1981; Wickstrom *et al.*, 1984; Parker *et al.*, 1999; Cook *et al.*, 2016; Denryter *et al.*, 2022b).

The Phenological Mismatch Paradox

Food supplies at northern latitudes undergo

dramatic seasonal changes in quality and quantity that can have different temporal peaks. Food quality and quantity typically reach a nadir during winter and a zenith during spring-summer (Parker *et al.*, 1999, 2009). The phenology of quantity and quality peaks differs, with food quality typically peaking earlier in summer than food biomass (Larter & Gates, 1991; Johnson *et al.*, 2022). When peaks in food quantity and quality and nutritional demands of herbivores are temporally discrete, a mismatch may occur (Post & Forchhammer, 2008). Phenological mismatches between food quality and quantity beg the question as to how ungulates achieve adequate energy and protein intake when the timing of peaks in these forage characteristics differ.

The basic assumptions of the Phenological Mismatch Paradox are that (1) ungulates meet nutritional requirements at highest forage quality and (2) as forage quality declines, ungulates can no longer meet their requirements despite increasing biomass. However, ungulates may not always meet their requirements when forage quality is highest, such as during spring because of physical and physiological constraints on food acquisition and digestion. For example, during late gestation and early lactation when food quality is typically at its highest, voluntary intake of food decreases, in part because of fetal compression of the rumen and hormone-induced changes in appetite that continue for up to a week following parturition (Lenkeit *et al.*, 1966; Forbes, 1970, 1987; Marsh *et al.*, 1971; Ingvartsen *et al.*, 1992). Thus, during late gestation and early lactation, females may not be fully able to take advantage of available high-quality forage. Additionally, even as quality declines through summer, it can remain above requirements until late in the season (Parker *et al.*, 1999; Cook *et al.*, 2016; Denryter *et al.*, 2022b).

The functional response also is important in considering whether ungulates can meet their nutritional requirements, even when food quality peaks. The functional response is largely dictated by the density of available foods (Solomon, 1949; Holling, 1959) and its effects on bite mass and bite rate (Trudell & White, 1981; Wickstrom *et al.*, 1984; Spalinger & Hobbs, 1992; Denryter, 2017). Despite high forage quality in spring-early summer, intake rates are often not at peak levels at this time because food intake is constrained by how fast animals can acquire food. Foods providing larger bite masses, such as those that are further in development phenologically, contribute to higher rates of intake (Spalinger & Hobbs, 1992; Shipley & Spalinger, 1992; Cook *et al.*, 2016; Denryter, 2017). As bite mass decreases, ungulates increase bite rates, but increased bite rates generally cannot fully compensate for smaller bite masses (Spalinger *et al.*, 1988; Spalinger & Hobbs, 1992; Rominger *et al.*, 1996; Cook *et al.*, 2016; Denryter, 2017). Thus, ungulates take advantage of peaks in biomass, which afford larger bites, to achieve even higher total nutrient intakes compared to when quality peaks.

We illustrate the relationship between biomass and daily energy intake with data approximated from Johnson *et al.* (2022) on digestible energy and forage biomass on caribou range in Alaska and functional response data for caribou in British Columbia (Denryter, 2017). In 2019, peak digestible energy values were ~10.7 kJ/g of food and biomass at that time was ~270 kg/ha (Johnson *et al.*, 2022), which gives a dry matter intake of ~3.8 g/min (Denryter, 2017). Assuming 13 h/day foraging during summer, daily intake of digestible energy would be ~32,000 kJ (3.8 g/min * 13 h * 60 min/h * 10.7 kJ digestible energy/g). Peak biomass levels several weeks later approximated 500 kg/ha, at which time digestible energy values were ~10.2 kJ/g. Given an associated dry matter intake of ~4.5 g/min at ~500 kg biomass, daily intake of digestible energy approximates

36,000 kJ–a difference of ~4,000 kJ compared to intake at peak quality. Although these modeled values are crude approximations combined from disparate studies, they illustrate the importance of increasing levels of biomass in meeting nutritional requirements even as diet quality declines. Such findings are consistent with some predictions of the forage maturation hypothesis, in that intake is maximized relative to constraints imposed by the interaction between forage quality and quantity (Fryxell, 1991; Hebblewhite *et al.*, 2008). The ability to meet nutritional requirements across a range of available quality and quantity thus resolves the phenological mismatch paradox.

Selective foraging also allows northern ungulates to tolerate phenological changes in forage quality and quantity. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) and caribou switch from diets dominated by deciduous shrubs, forbs, and mushrooms in summer-autumn to diets with large proportions of lichens during winter (Thing, 1984; Russell *et al.* 1993, Thomas *et al.*, 1996; Parker *et al.*, 1999; Denryter *et al.*, 2017). In contrast, moose selected woody browse species throughout the year but consumed large quantities of fireweed (*Chamerion angustifolium*) when it was available during summer (LeResche & Davis, 1973; Wam & Hjeljord, 2010). Wood bison (*Bison bison athabascae*) switched from a sedge-based winter diet to a more diverse summer diet that also included willows (*Salix* spp.; Larter & Gates, 1991). Selective foraging within and among seasons allows northern ungulates to achieve the highest relative quality available, which contributes to significantly greater daily mass gains (e.g., >200%) compared to non-selective foraging (White, 1983).

Studies aiming to evaluate whether phenological mismatches limit northern ungulates should incorporate nutritional requirements and compare how changes in forage quality across the season affect the ability of animals to meet nutritional requirements. Additionally, nutrition studies focused on phenology should incorporate information on the functional response, which can serve as a basis for understanding how changes in forage quantity and quality affect the ability of ungulates to meet nutritional requirements. Nutrition and phenology studies represent another application for tame animals in field settings, which can allow for estimation of the functional response needed to quantitatively link changes in phenology to changes in nutrient intake and other nutritional outcomes (e.g., White *et al.*, 1975; Wickstrom *et al.*, 1984; Parker *et al.*, 1999; Cook *et al.* 2016; Denryter, 2017).

The Green World Paradox

In their classic work, Hairston *et al.* (1960) concluded that herbivores generally were not limited by food supplies. Their work, known as *The Green World Hypothesis*, was based on observations that plants rarely are depleted by herbivores and instead are usually abundant and relatively intact, except in a few extreme cases. Nutrition has since been demonstrated to be a bottom-up limiting factor for many northern herbivores (White *et al.*, 1975; Dale *et al.*, 2008; Cook *et al.*, 2013; Hurley *et al.*, 2014; LaSharr *et al.*, 2023a). Nonetheless, questions persist about how nutrition can be limiting when the landscape is green with an abundance of plants. For example, increasing plant biomass in the Arctic has been associated with "paradoxical" population declines of caribou (Fauchald *et al.*, 2017). The basic assumption of the Green World Paradox is that all green vegetation is food, and if green vegetation is available, then ungulates cannot be nutritionally limited. In reality, not all green vegetation is food because ruminants are highly selective foragers (Skogland, 1980; White & Trudell, 1980; Weckerly, 1994) and avoid many available species (Fig. 2). For example, tame elk (*Cervus elaphus*) selected only a fraction (42) of 206

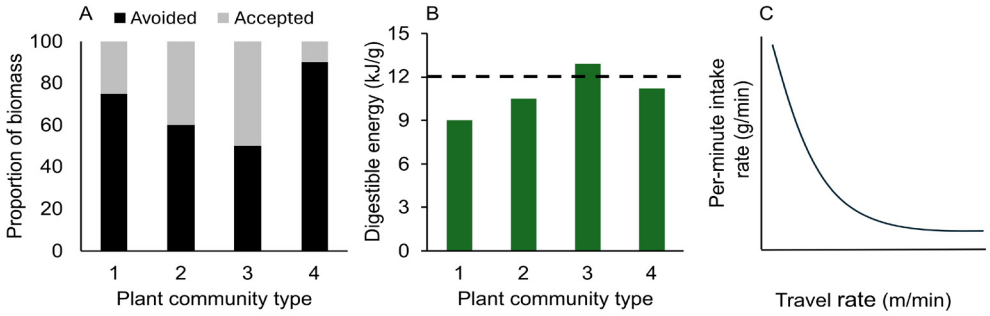

Figure 2. Contradictions underlying the Green World Paradox are resolved by the fact that not all green biomass is accepted as food by northern ungulates, as illustrated for 4 unique plant communities (A), that not all vegetation provides adequate nutrients to meet nutritional requirements (depicted by the dashed line; illustrated for 4 plant communities (B)), and that food can be distributed in ways that make foraging inefficient by causing searching for food, as indicated by travel rates, to compete with intake (C).

available species (Cook *et al.*, 2016) and tame caribou accepted <50% of available biomass as food (Denryter *et al.*, 2017).

Food quality also is important for understanding the nutritional value of a landscape to a ruminant herbivore because quality influences digestion. Lower-quality, less-digestible foods take longer to break down to a particle size that can pass from the rumen to the reticulum and therefore have longer passage rates and retention times in the digestive tract (Poppi *et al.*, 1981; Bryant *et al.*, 1991; Illius & Gordon, 1992; Tafaj *et al.*, 2005). Because the rumen is limited by capacity, new food cannot enter the rumen until enough previously ingested food has passed through it, so foods that take longer to digest (i.e., are lower in quality) reduce the amount of food that can be consumed during a given period (Welch, 1982; Lechner-Doll *et al.*, 1991). Ruminants have some flexibility to accept foods that are marginally below requirements for dietary concentrations of nutrients (Denryter *et al.*, 2022*b*), and in winter it is expected that forage quality will be below requirements. Significant deviations from required dietary concentrations of nutrients, however, constrain daily intake and result in nutritional limitations (Cook *et al.*, 2004).

Some plants are not palatable or nutritious because they contain high amounts of plant secondary metabolites (PSMs), which help defend plants against herbivory; in some cases, herbivory even initiates synthesis of PSMs. PSMs are antinutritional factors that interfere with digestion to varying degrees (e.g., tannins), or that can be toxic or even lethal if consumed (e.g., alkaloids found in lupine (*Lupinus* spp.; Robbins *et al.*, 1987; McSweeney *et al.*, 2001; Min *et al.*, 2003; Raisbeck *et al.*, 2011)). Tannins occur in the leaves of many woody browse species and some forbs, which make them consequential for northern ungulates consuming these foods. When an ungulate consumes a diet high in tannins, it may lose more protein processing the tanniferous forage than is gained, resulting in negative protein intake (Robbins *et al.*, 1987: McArt *et al.*, 2009; Spalinger *et al.*, 2010; Denryter *et al.*, 2022b). Although some herbivores have evolved salivary proteins that bind to plant tannins, thereby reducing nega-

tive effects on digestion, other ungulates may struggle to meet requirements on diets containing large quantities of tannins (Hagerman & Robbins, 1993; McArt *et al.*, 2009). PSMs thus deter ungulates from consuming some forages, thereby reducing what vegetative biomass ungulates accept as food.

The availability and distribution of foods across the landscape for northern ungulates also are important in determining whether a green world can be limiting. Spatial distributions of available foods control foraging efficiency and the functional response; poor spatial distributions of food can limit the ability of ungulates to exploit foods effectively. When food densities are low, foraging inefficiencies can arise from competition between searching for and acquiring food (Cook *et al.*, 2016; Denryter, 2017; Denryter *et al.*, 2020) (Fig. 2). When food is sparse or patchily distributed, northern ungulates may not be able to satisfy nutritional requirements because of resultant foraging inefficiencies that constrain the functional response, thereby limiting rates of nutrient acquisition. Additionally, factors such as parasites or predation risk may cause ungulates to avoid certain parts of the landscape (Gunn & Irvine, 2003; Cuyler *et al.*, 2012; Viejou *et al.*, 2018). Thus, even if the green world has plentiful vegetation, ungulates may struggle to acquire adequate amounts of food.

Sampling to understand how nutrition can limit ungulates in a green world requires incorporating information on forage selection so that biomass sampling can be targeted to the species used as food by the forager of interest. Not all accepted biomass will likely be used by foragers for reasons discussed above, which makes estimating nutritional carrying capacity a persistent challenge. Studies that can incorporate information on what constrains forage use and the functional response, including food quality and distributions, plant architecture, and predation risk, will provide better insights into how northern ungulates are constrained by their environments.

The Paradox of Pregnancy Rates

A common assumption about wild populations is that if pregnancy rates are high, then nutrition is not limiting. The basic assumption for this paradox is that pregnancy is indicative of maternal nutritional state because the probability of pregnancy is influenced by nutritional condition (as indicated by body fat) (Thomas, 1982; Gerhart *et al.*, 1997a; Cook *et al.*, 2004; Stephenson *et al.*, 2020). However, neither body fat nor body mass directly regulate fertility (Bronson & Manning, 1991; Gerhart *et al.*, 1997a). The importance of body fat in fertility likely arises in its role as part of an animal's total energy balance, which better predicts ovulation and fertility than body fat or mass alone (Bronson & Manning, 1991). Some non-nutritional factors such as diseases (e.g., brucellosis) and parasites (e.g., *Neospora caninum*) also can affect probability of pregnancy and are associated with higher risk of abortion (Hughes *et al.*, 2009; Carlsson *et al.*, 2019). Another issue in using pregnancy rates to evaluate nutrition is that there is no standard definition of "high" pregnancy rates, which makes interpretations of pregnancy rate subjective and potentially detached from nutrition. The seminal work of Cook *et al.* (2004) explored the effects of nutrition on reproduction and performance in elk. Adult and yearling elk in 'excellent' and 'good' nutrition treatments achieved pregnancy rates of ≥90%; pregnancy rates declined with worsening nutrition, but adult pregnancy rate was one of the least sensitive indicators of nutritional condition (Cook *et al.*, 2004). In a vastly different study, 100% of yearling caribou achieved pregnancy (age of first breeding at 1.5 years old, first birth at 2 years old) when summer and winter ranges were high in nutritional quality (Ouellet *et al.*, 1996). From these studies, a reasonable thresh-

old for high pregnancy rates may be ≥90% in adult and yearling cervids. High pregnancy rates, however, do not necessarily negate the presence of nutritional limitations.

Pregnancy rates can be high when nutrition is limiting in at least three scenarios. First, pregnancy rates can be high when nutritional limitations are moderate, affecting total energy balance, but not enough to cause a reduction in probability of pregnancy (Eberhardt, 2002). Second, in systems where juvenile mortality before weaning is high, nutritional limitations can be masked when reproductive females are released from the high nutritional demands of lactation after losing a calf (Gerhart *et al.*, 1997*b*; Dale *et al.*, 2008). With demands for milk production diminished, "released" females can invest in additional fat accretion. Thus, when juvenile mortality is high, a large proportion of females should be in adequate nutritional condition to breed in autumn (Gerhart *et al.*, 1997b; Dale *et al.*, 2008). Third, nutrient flushing, in which an increased plane of nutrition is available to animals at the time of breeding, promotes ovulation and fertility, especially in animals in poorer nutritional condition (I'Anson *et al.*, 1991), and can thereby increase reproductive rates (Gunn *et al.*, 1969) (Fig. 3). Pulses of mushrooms and green up of graminoids following autumn rains are thought to be important natural flushing events for various northern ungulates (White *et al.*, 1993; Cook *et al.*, 2011, 2013).

Another challenge in interpreting information on pregnancy rates is that often there is no distinction made between pregnancy rates of lactating and non-lactating females. Lactating females require approximately twice as much energy and protein as non-lactating females to achieve the same level of fat and mass gain (Oftedal, 1985; Robbins, 1993; Cook *et al.*, 2004; Denryter *et al.*, 2020, 2021). During early lactation, which often occurs prior to green up and peak biomass, lactating females act as capital breeders, mobilizing fat and protein stores to support milk production, which increases their fat deficit compared to non-lactating females. Hence, lactating females must recoup more energy and protein than their non-lactating counterparts over summer

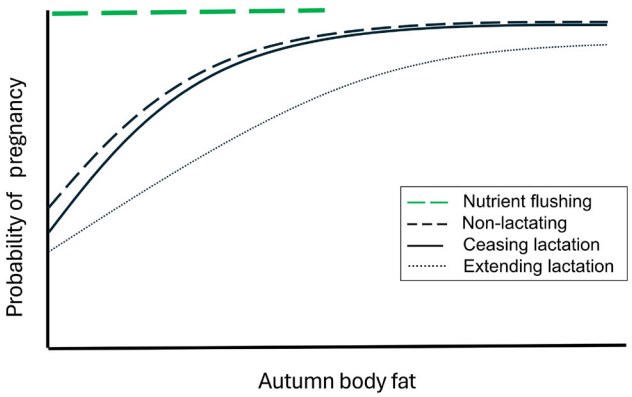

Figure 3. Predicted relationships between the probability of pregnancy and body fat for non-lactating females (black, dashed line), females ceasing lactation prior to conception (black, solid line), females extending lactation through winter (black, dotted line), and for thin females that can take advantage of forage nutrient flushing (green dashed line).

(Oftedal, 2000), which contributes to lactating females being more sensitive to nutritional limitations than non-lactating females (Gerhart *et al.*, 1997b; Cook *et al.*, 2004). Unless the summer-autumn range provides a high plane of nutrition, non-lactating females will accrete fat more readily than lactating females (Cook *et al.*, 2004), which is a relatively ubiquitous phenomenon (Crête & Huot, 1993; Cook *et al.*, 2021; White *et al.*, 2014; Stephenson *et al.*, 2020; Smiley *et al.*, 2022).

The significance of differences in body fat levels between lactating and non-lactating animals is apparent when examining relations between body fat and pregnancy (Fig. 3). Higher body fat levels (as they influence total energy balance) often are associated with higher probability of pregnancy (Gerhart *et al.*, 1997b; Cook *et al.*, 2013; Stephenson *et al.*, 2020). If non-lactating females are more likely to achieve a higher level of body fat needed to breed because of their lower nutritional requirements than lactating females, they may achieve higher rates of pregnancy. If lactating females cannot accrete the same amount of body fat as non-lactating females, they may instead go through a reproductive pause in which they do not breed that year (Cameron, 1994; Cameron & White, 1996), which minimizes wasted reproductive investment and provides nutritional relief needed to enhance success in subsequent reproduction (Cameron, 1994; Hamel *et al.*, 2011; Monteith *et al.*, 2013; Smiley *et al.*, 2022). Hence, pregnancy rates of lactating females would be depressed compared to non-lactating females. In these situations, non-lactating females will inflate estimates of population-level pregnancy rates, which could lead to erroneous conclusions about the nutritional status of the population. Gerhart *et al.* (1997b) summarized the issue as follows:

> "Pregnancy rate determined from females sampled randomly [without considering lactation status] may lead to erroneously high estimates of nutrient availability and an overly optimistic potential for population increase relative to evaluations based on lactating females."

The complicated relations among nutrition, pregnancy, reproductive history, predation, disease, and other factors highlight why relying on high pregnancy rates alone to index nutritional status of populations can be misleading. Studies aiming to evaluate potential nutritional constraints should consider pregnancy rates in the context of other (non-nutritional) factors that influence pregnancy and previous recruitment, recognizing that regardless of nutrition, pregnancy rates are likely to be higher in populations with low levels of recruitment.

The Population Persistence Paradox

Nutrition is the foundation of populations through influences on vital rates, such as pregnancy, age of first reproduction, juvenile survival, and adult female survival, that influence population rates of change (Gaillard *et al.*, 2000). By definition, virtually every ungulate population will experience some level of nutritional limitation because resources are not unlimited. The Paradox of Population Persistence stems from the assumption that nutritional limitations cause a population to collapse because of unsustainable reductions in vital rates. That assumption may arise from observations of rapid and dramatic population declines triggered by density-dependent nutritional limitations (Couturier *et al.*, 1990; Klein, 1991; Crête & Huot, 1993; Bergerud *et al.*, 2008), in which ungulate populations destabilize plant communities and overshoot nutritional carrying capacity (Hobbs, 1996). Severe weather also can rapidly and dramatically influence populations through effects on nutrition, in a density-independent manner, by increasing energy expenditures or limiting access to food (Fancy & White, 1987; Dailey & Hobbs, 1989; Parker,

1989). For example, heavy snowfall can have catastrophic effects on survival in small populations, especially if populations lack an adequate nutritional buffer (Conner *et al.*, 2018; Denryter *et al.* 2022a). Similarly, delayed snowmelt in spring contributes to higher mortality related to starvation (Dumont *et al.*, 2005; Jacobson *et al.*, 2004). Cumulative effects of severe winters can negatively affect population growth (Patterson & Power, 2002), though impacts vary relative to population age structure (Coulson *et al.*, 2000). Although extreme situations, including rain on snow and icing events, can precipitate severe population declines, we are unaware of any modern examples of the extirpation or extinction of populations of northern ungulates owing solely to nutritional limitations.

Not all nutritional limitations result in population-level impacts, which is an important distinction that may underpin the perception that nutritional limitations for northern ungulates are paradoxical. Instead, nutritional limitations often are more insidious, being signaled through reduced performance (Cook *et al.*, 2004). Age of first reproduction generally increases when nutrition is limiting because females take longer to achieve body mass and fat levels that support breeding (Reimers, 1983; Gaillard *et al.*, 1992; Jorgenson *et al.*, 1993; Saether & Heim, 1993; Strickland *et al.*, 2008; Martin & Festa-Bianchet, 2012). Nutritional limitations contribute to lower probability of pregnancy, higher rates of reproductive pauses, and production of fewer offspring (Cameron, 1994; Gerhart *et al.*, 1997a; Cook *et al.*, 2013). Embryonic mortality can increase owing to inadequate fat reserves to simultaneously support gestation and maternal survival (Russell *et al.*, 1998), although abortions are rare and may be limited to extremely severe nutritional restriction (Cook *et al.*, 2002). Offspring produced during periods of nutritional limitation are smaller, born later, and more vulnerable to mortality than their larger, earlier-born counterparts (Keech *et al.*, 2000; Cook *et al.*, 2004), in part because maternal nutrition required to ovulate and support fetal growth is limited (Allaye Chan, 1991). As nutrition declines, polytocous species that usually produce >1 offspring at a time, such as deer and moose, tend to produce fewer offspring (Keech *et al.*, 2000), although litter size can be inconsistent with individual nutritional condition (Monteith *et al.*, 2014). Growth and development of juveniles also may be depressed when nutrition is limiting (Reimers, 1983; Crête & Huot, 1993; Cook *et al.*, 2004; Long *et al.*, 2019), especially given that milk production also is reduced (Rognmo *et al.*, 1983; White & Luick, 1984; White, 1992; Chan-McLeod *et al.*, 1994). Reduced rates of growth result in smaller body size and fewer body stores of offspring entering winter, which decreases probability of survival through winter (Clutton-Brock *et al.*, 1983, 1987; Loison *et al.*, 1999; Cook *et al.*, 2004; Taillon *et al.*, 2006) and lowers recruitment (Shallow *et al.*, 2015; Scornavacca *et al.*, 2016; Jackson *et al.*, 2021). Additionally, poor nutrition can increase susceptibility to other sources of mortality (Clutton-Brock *et al.*, 1983; Rognmo *et al.*, 1983; Skogland, 1990; Fairbanks, 1993; Mech, 2007; Bender *et al.*, 2008; Smiley *et al.*, 2024). In the most severe cases, nutritional limitations contribute to reduced survival of adult females (Denryter *et al.*, 2022a; LaSharr *et al.*, 2023a). If enough individuals experience nutrition-related reductions in performance, the finite rate of population increase (λ) may be reduced (Monteith *et al.*, 2014; Stephenson *et al.*, 2020). Thus, the result of nutritional limitations often is an overall reduction in individual performance and population productivity.

Reductions in performance and productivity do not necessarily equate to extirpation or extinction and in some cases may enable population persistence. Nutritional requirements for reduced performance and productivity are lower than for higher performance and pro-

ductivity, which may better allow individuals in nutritionally limited populations to meet requirements from the available forage base. Over time, nutrition-related reductions in performance to individuals may result in smaller body size or body-size related traits (Reimers, 1983), as in black-tailed deer (*O. h. columbianus*) (Long *et al.*, 2019) and Peary caribou (*R. t. pearyi*) (Thomas & Everson, 1982). Smaller body size is advantageous when food is limited and may even result in greater food-processing efficiency (Ullrey *et al.*, 1967; Verme & Ullrey, 1984; Demment & Van Soest, 1985; Illius & Gordon, 1992; Vijendravarma *et al.*, 2012; Little, 2020). Increased food-processing efficiencies could allow individuals to tolerate nutritional limitations without necessarily reducing performance or productivity. Additionally, ungulate populations may exhibit increased migratory propensity (Fryxell & Sinclair, 1988; Denryter *et al.* 2024) or change their spatial distribution through time (Collins *et al.*, 2011), or they may stabilize at lower densities (Seip & Cichowski, 2006; Bergerud *et al.*, 2008), which could aid population persistence. Nutritional limitations may be only periodic or temporary (e.g., following droughts, wildfires, or overshoots of carrying capacity) or they may not be realized at the population level if the limitations are too small to affect demographic rates. Extirpation and extinction become a concern primarily when nutritionally limited populations are vulnerable to other limiting or regulating factors (Murray *et al.* 2006; Maublanc *et al.*, 2009; DeCesare *et al.*, 2025). Studies aiming to evaluate how populations can persist despite nutritional limitations must differentiate between nutritional limitations at the level of the individual and the level of the population, which can be accomplished by relating measures of nutrition to vital rates and λ.

Conclusions

Life in highly seasonal environments necessitates acquisition, storage, and conservation of surplus nutrients to ensure survival and reproduction. Northern ungulates often meet those needs through adaptations including selective foraging, migration, biochemistry, and seasonal changes in metabolism, even when faced with imbalanced diets and phenological changes in forage quantity and quality. When physiological and behavioral adaptations are inadequate to support meeting nutritional requirements for survival and reproduction, northern ungulates become less productive as manifested through changes in life-history traits, such as decreased body mass, slower growth, delayed age of first reproduction, and reproductive pauses. Collectively, the physiological, behavioral, and life-history adaptations of northern ungulates allow them to persist during periods of nutritional limitation and allow for the resolution of many nutritional paradoxes.

Understanding the role of nutrition in the ecology of northern ungulates is contingent upon recognizing various adaptations to life in seasonal environments but also requires designing studies appropriately. If the goal is to evaluate whether a population is nutritionally limited, the appropriate technique to employ would be evaluating nutritional condition of individuals (at the time of year that reflects the season(s) of limitation), as opposed to performing only habitat assessments, which do not provide a direct link to animal performance. Incorporating nutritional concepts into ecological studies more holistically will help define the relative importance of nutrition. Most populations of northern ungulates will experience periods when nutrition is limited (Parker, 2003), but not all nutritional limitations will result in population-level impacts. Failing to recognize the role of nutrition in the ecology of northern ungulates may lead to erroneous conclusions that result in ineffective or counterproductive conservation and management actions. Even when nutritional limitations occur, they do not

preclude the influence of other factors in limiting or regulating populations; rather they may exacerbate the effects of other factors, making it even more important to understand the role of nutrition. A strong foundational knowledge of nutritional ecology and associated adaptations of ungulates can help ensure nutritional limitations are not overlooked.

Dedication

We dedicate this overview of nutritional paradoxes for northern ungulates to Donald E. Russell. Once described as a luminary among Arctic animal ecologists, Don endeavored to understand the Porcupine Caribou Herd. He communicated that story through principles of nutritional ecology. His initial modelling approach involving feeding behavior in relation to rumen function and activity budgets was incorporated into a comprehensive energetics analysis in the range ecology study of the Porcupine Caribou Herd. This study integrated feeding activity, vegetation selection, distribution and movements to predict energy intakes, digestibility and energy balance, and seasonal reserves of body fat in relation to fecundity. Following research on the importance of breeding pauses in Arctic caribou, Don and Robert White incorporated the role of protein into their energetics modelling framework to evaluate use of body reserves during gestation and lactation as drivers of vital rates, weaning success and long-term reproductive strategies. Don used the modeling approach to project population responses and evaluate impacts to caribou of mineral and oil extraction in Arctic Canada and Alaska. His work continues to be fundamental to caribou conservation.

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