

The complexity of interacting nutritional drivers behind food selection, a review of northern cervids

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Abstract. The research literature on food selection by large herbivores is extensive. Still, we are generally lacking in our knowledge of the influence of potentially interacting chemical contents of the food. We made a qualitative review of a systematic literature search of studies that empirically link chemical contents of food to the food selection by northern cervids (genera *Alces*, *Capreolus*, *Cervus*, *Dama*, *Odocoileus*, *Rangifer*). We found that although the majority of the 98 relevant studies measuring any given food constituent (energy, protein, fiber, minerals, plant secondary metabolites) provided support for it acting as a driver of food selection (in either a negative or positive way), there was little support for the traditional hypotheses of maximization or limitation of any single constituent. Rather, because of the animals' need to acquire an appropriate intake of several constituents at the same time, our review highlights how new empirical studies need to focus on several food constituents in synchrony: (1) Study designs should capture sufficient variation in the content of food constituents in order to tease apart their many co-variations; and (2) insights about nutritional drivers may be lost if one uses only composite currencies such as crude energy, crude fiber, ash, or tannins, which may mask contrasting selection patterns of the lumped constituents. Season had an apparent influence on the selection of some food constituents, particularly various fiber fractions. In contrast, our review revealed a lack of evidence that cervids more strongly select for protein in summer than they do in winter. Our overall conclusion of the review is that interacting chemical contents of food make the nutritional value of a given food type into a varying entity. To better elucidate this variation, we need new technologies that non-invasively capture nutrient intake of free-ranging animals, across seasons.

Key words: caribou; deer; elk; feed; fitness; macronutrient; maximization; moose; nutritional ecology; optimal foraging.

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INTRODUCTION

Food selection by large herbivores shapes the distribution of both plants and animals across the globe (McLaren and Peterson 1994, Maron and Crone 2006, Speed and Austrheim 2017). To manage our sustenance of such ecosystems, we need to know what the animals choose to eat, when, and where. Decades of extensive research have clarified why the answer is so context-dependent: Animals make foraging decisions on many spatiotemporal scales, trading off the quality and quantity of available food against the energy spent to obtain it (Senft et al. 1987, Searle et al. 2006), as well as non-dietary risks such as predation and weather (Hebblewhite and Merrill 2011). For example, herbivore food selection is influenced by interrelated variables such as plants' spatial distribution, biomass, morphology, and bite sizes (Spalinger and Hobbs 1992, Shipley et al. 1998, Stolter 2008, Wam and Hjeljord 2010). Even the chemical contents of food (here: food constituents) interact and may make the apparent nutritional value of a given food type non-fixed, varying with the nutritional status of the consumers (Provenza 1995, Simpson and Raubenheimer 2012, Felton et al. 2016, Wam et al. 2018).

Nutritional ecology concerns the nutritional links between the environment and an animal's food intake, and its resultant physiological state. These interactions are based on the underlying need for individuals to obtain appropriate quantities of certain food constituents, given the various kinds of constraints imposed on them by their physiology and the external environment (Parker 2003). Different individuals may prioritize different food constituents when choosing the foods and amounts they consume (i.e., their nutritional strategy), due to variations in body size, metabolic adaptations, life history, and physiological states (Jarman 1974, Parra 1978, Van Soest 1994, Müller et al. 2013). For example, because energy and protein are necessary for building new tissue, we expect size and sex to influence the animals' selection for it (Staines et al. 1982, Padmalal and Takatsuki 1994, Luna et al. 2013). On the other hand, pregnancy, for example, may also incur an improved metabolic utilization of protein (Monteith et al. 2014), which may in part negate the need to select for food of higher protein (no sex

differences were found by, e.g., Weckerly and Nelson 1990, Jiang et al. 2009). Most large herbivores also must cope with large seasonal differences in food availability, for which they are physiologically adapted (Moen 1978, McMahon et al. 1997). In this context, northern browsers and some mixed feeders (*sensu* Hofmann 1989) face a particularly large variation in both food availability and quality because they eat completely different food types in winter (mainly twigs) and summer (mainly leaves and forbs).

Each food package an animal selects to eat in any season offers a unique combination of food constituents. Typically, the different constituents co-vary with each other in the food package, making it tricky to discern which constituent, or combination/balance of constituents, drives food selection (Makkar and Singh 1995, Rothman et al. 2012). For example, a significant negative co-variation between nitrogen and acid detergent fiber (ADF) was found across leaves of 443 plant species frequently eaten by various herbivore species on three continents (Wallis et al. 2012). Similarly, a significant positive co-variation between nitrogen and phosphorous concentrations was found across leaves from 2548 species from 219 families at 175 sites across the world (Wright et al. 2004). Sometimes the ingestion of one type of food affects the ingestion or digestion of another (DeGabriel et al. 2014). For example, the effects of plant secondary metabolites (PSM) on an herbivore's physiology may be closely linked to the balance of nutrients in the food ingested (Simpson and Raubenheimer 2001, Villalba and Provenza 2005, Au et al. 2013).

Despite—or maybe rather because of—all this complexity in the nutritional underpinnings and the variation among animals in feeding needs and constraints, several theories have been put forward to generalize the nutritional strategy of a given animal species, including the following: (1) energy maximization (Schoener 1971, Belovsky 1978); (2) protein maximization (Mattson 1980); (3) regulation or limitation of dietary fiber (Jones 1972, Van Soest 1994); (4) regulation or limitation of minerals (Robbins 1994); (5) regulation or avoidance of plant secondary metabolites (Free-land and Janzen 1974); or (6) nutrient balancing (Westoby 1974, Simpson and Raubenheimer 2012). Tests of these hypotheses have produced a wide range of conclusions, and there is a need to

systemize the available data (DeGabriel et al. 2014).

Here, we synthesize the body of empirical studies conducted into the nutritional underpinnings of food selection by cervid ruminants (*Cervidae*) in the Northern Hemisphere (species having the majority of their natural occurrence at latitudes >30° N). We limited our review to the northern cervids in order to reduce the number of influential factors, but still retaining adequate amounts of literature. We try to answer systematically to which extent northern cervids fit into each of the six different nutritional strategies introduced above (1–6). We do this by tabulating the studies' conclusions about the driving role of a given food constituent (macronutrients, minerals, or plant secondary metabolites), and how these conclusions depended on which other constituents were measured in the study. This is to highlight how nutritional drivers can interact with each other. We purposely avoid using the number of papers to infer which driver is the more important, given science's general underreporting of negative results. Such underreporting may not apply equally to food constituents because they are addressed largely by different research paradigms (1–6 above). We relate our findings qualitatively to context-dependent factors such as season, size, and physiological state, but we do not systemize their influence. In this complex field with many interactive processes, comparing single metrics across vastly different study designs could be misleading (CEE 2013). Because study design has defining influence on

conclusions about food selection (Felton et al. 2009a), we categorized studies into one of three types of inquiry to systemize their results (Table 1).

METHODS

To retrieve relevant literature, we systematically searched two databases: Web of Science (<http://www.isiwebknowledge.com/>) and Scopus (<https://www.scopus.com>). The searches were conducted on 24 August 2016. In Web of Science, we used the following Boolean search terms: Topic: (*alces* OR *capreolus* OR *dama* OR *odocoileus* OR *rangifer* OR *cervus* OR moose OR "roe deer" OR "red deer" OR elk OR reindeer OR caribou OR "white-tailed deer" OR "sika deer" OR "fallow deer" OR "sitka deer" OR "black-tailed deer" OR "wapiti" OR "mule deer") AND Title: (brows* OR food* OR forag* OR diet* OR nutri* OR feed*). We checked the search with and without hyphens for each of all two-word search terms and found only one additional (not relevant) paper due to a hyphenation of sika deer. The same search terms that were used for Topic in Web of Science were used in a combination of the Scopus' search fields Title, Key words, and Abstract. The same search terms that were used for Title in Web of Science were used in Scopus search field Title. Note that in the text, we avoid the ambiguous term "elk" and use wapiti as common name for *Cervus canadensis* (previously *C. elaphus*) when the main range of the study animals was in North

Table 1. The three types of inquiry we used to classify relevant empirical studies in this review of the nutritional drivers behind the food selection of northern cervids (modified from Felton et al. 2009a).

Types of inquiry	Examples of specific methods
(A) Selection or preference studies: Researchers relate the nutritional contents of food items to selection or preference by the animals	Comparisons of the nutritional composition of food items (e.g., plant specimens, plant species, composite samples from feeding plots) combined with a measure of food use relative to availability (e.g., selectivity indices like Ivlev's, browsing intensity, and preference ranking)
(B) Intake rate studies: Researchers relate nutritional contents of food items to individuals' (daily or near-daily) food intake	Observations of animals, by direct observation or camera surveillance; coupled with data on nutritional composition of food to measure intake of various food constituents. In captivity, intake rates can also be quantified by weighing trays before and after feeding
(C) Circumstantial evidence studies: approaches other than A or B	For example, observations of time spent by animals in habitats offering different nutritional composition of available food, or nutritional composition of discarded food in ad libitum feeding experiments

America and eastern Asia, and red deer for *Cervus elaphus* when the main range was in Eurasia. We only included peer-reviewed papers written in English. We included studies on animals in captivity, as they can facilitate our understanding of free-ranging cervids. We make clear throughout the text whether findings stem from captive animals.

The search resulted in 2681 search hits in Web of Science and 2235 search hits in Scopus. The overlap between the two searches was substantial, and the total number of unique search hits was 2944. In a first selection round, we distributed search hits evenly among us and discarded those that were clearly not relevant, based mainly on titles or abstracts. The remaining 827 search hits in Web of Science, and the additional 74 search hits that we found in Scopus, but not in Web of Science, were read in depth by at least one of the co-authors. We regarded as relevant empirical peer-reviewed studies that statistically linked food selection to nutritional content of the food. The final 98 papers included as a basis for the review are listed in Appendix S1. Note that in the text, we include papers additional to the 98 in Appendix S1 to aid our discussion (papers on physiology, generic reviews, etc.).

Acknowledging that the terms “use,” “selection,” and “preference” are ambiguously applied in the literature (Hall et al. 1997), we here define them as follows: Use is simply that a food type is eaten (irrespective of what the animal has to choose from), while selection is the decision animals make about use relative to availability (Johnson 1980). Studies reporting use without somehow relating it to this element of choice are of little relevance for understanding nutritional drivers (and not included among our relevant 98 reviewed papers). A food type used more often than expected from its availability we call a selected or preferred food type. We use the term preference (or preferred) for feeding choices made under conditions where all types are of equal or almost equal availability, whereas selection (or selected) refers to feeding choices where food types were available at unequal, but known/estimated amounts (Thomas and Taylor 1990). The former typically involves some kind of cafeteria trials, which can be performed with both captive and wild animals.

RESULTS AND DISCUSSION

The 98 publications included in our review reflect the circumferential distribution of cervids in the Northern Hemisphere (Fig. 1). A high share of the studies involved captive or tamed animals (58% overall, and 89% of studies with intake rates). The share was largely equal across studies addressing the various food constituents (range 33–62% overall). Few studies addressed selection of food constituents in relation to body size and/or sex, and we therefore refrain from drawing general conclusions regarding these factors. Of the three types of inquiry (Table 1), there were more studies of selection among food types (52%) than studies of food intake rates (37%) or studies with circumstantial evidence (11%). The majority of the papers measured either one (33%) or two food constituents (37%). No paper measured all five constituents of interest (Fig. 1).

Nutritional strategy (1–2): energy or protein maximizers?

Background: why should cervids select food high in energy or protein?—Energy constitutes the fuel of all organisms. It is important to remember that energy is not a nutrient per se, but a property of macronutrients (carbohydrates, proteins, and lipids for ruminants; Van Soest 1994). Early studies on food selection suggested that animals have evolved to maximize the net gain of energy within stipulated constraints, while minimizing time spent foraging which may expose them to predation and thermal imbalance (Belovsky 1978, Stephens and Krebs 1986). The energy needed for daily metabolic maintenance is fairly fixed for a given life stage (e.g., 0.39 MJ/kg^{0.75} body mass for adult non-lactating cervids in winter–spring), but there are large differences in the amount of additional energy needed due to activity, reproduction, and weather (Dryden 2011).

The same factors also influence the protein requirement of the animal, albeit not linearly with their influence on energy (Parker et al. 1999). Wild cervids require roughly 5% crude protein (CP) of dry matter intake for maintenance, but up to 25% for reproduction (Dryden 2011). Natural forage for northern cervids typically contains 5–15% CP, with rare extremes of 25–30% (Leslie et al. 1984, Sprinkle et al. 2002, Marshal et al. 2005, Marell

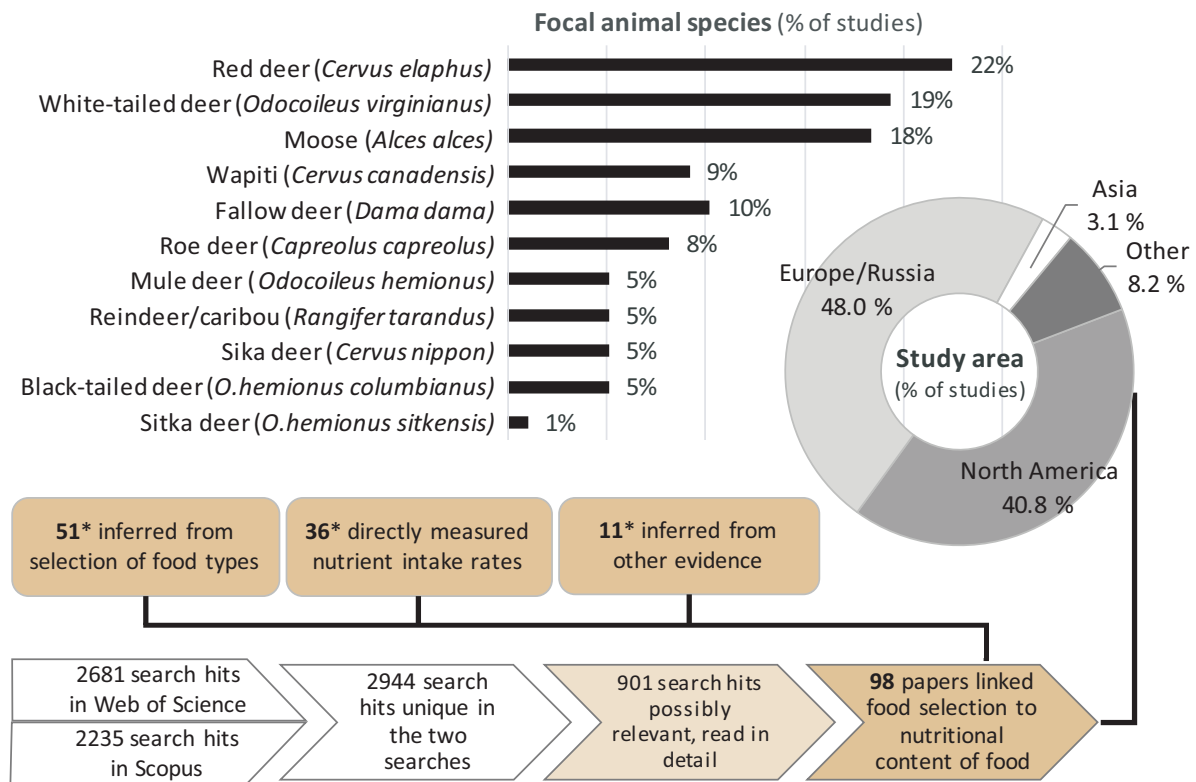


Fig. 1. Summary description of the literature search for empirical papers addressing nutritional drivers behind food selection by cervid ruminants (*Cervidae*) in the Northern Hemisphere (species having the majority of their natural occurrence at latitudes $>30^{\circ}$ N), using ISI Web of Science and Scopus, 2016. For search terms, see *Methods*. Asterisks indicate the number of papers among the final 98 that belonged to the three different types of inquiry (Table 1). Diagrams illustrate the relative representation of focal study areas (pie chart) and animal species (bar chart). Note that we use wapiti (not elk) as common name for *Cervus canadensis* (N. America, E. Asia) and red deer for *Cervus elaphus* (Eurasia).

et al. 2006, Wam et al. 2016). The much-quoted protein maximization hypothesis (Mattson 1980) postulates that many herbivores have evolved specific adaptations to get the most out of scarce levels of nitrogen in plant material. The rumen microbes can, for example, efficiently use ammonia when nitrogen in the food is scarce, and during excess nitrogen supply, additional nitrogen can be excreted as urea (Schwartz et al. 1987, Van Soest 1994). However, this regulating process requires glucose, adding intricacy to the links between requirements for—and utilization of—protein and energy.

Not all energy and protein in a plant are available to the animal, varying, for example, with amino acid composition (Robbins et al. 2005), fiber contents (Mason 1969, Besselmann 2005 in

Schwarm et al. 2009), or secondary metabolites that bind macronutrients (Robbins et al. 1987, Jones et al. 2010). Estimates of digestible energy and protein are therefore important for understanding food selection in individuals (Felton et al. 2009b, Ganzhorn et al. 2017). For example, if studies are limited to measures of crude or total energy, it is possible to overlook the different roles that the different energy-providing constituents may have, as well as potentially conflicting interactions with other nutritional constituents. Bomb calorimetry, for example, includes energy from lignin, a food constituent that appears to have a generally negative influence on food selection. It is for that reason surprising that in our review, the reported support for energy and protein being nutritional drivers

was only slightly different between studies with crude and digestible measures (Figs. 2a, 3a; note the relatively higher prevalence of crude measures for protein than for energy). One explanation may be that both in vivo and in vitro estimations of protein- and energy-digestibility are problematic to extrapolate to the population

level (though see Miller et al. 2009), because of complex interactions between diet and individual (Holand 1994, Storeheier et al. 2002, Villalba et al. 2002), and many of the studies in our review were compiled at the population level.

Here, we summarize findings of 74 empirical papers from our systematic search that address

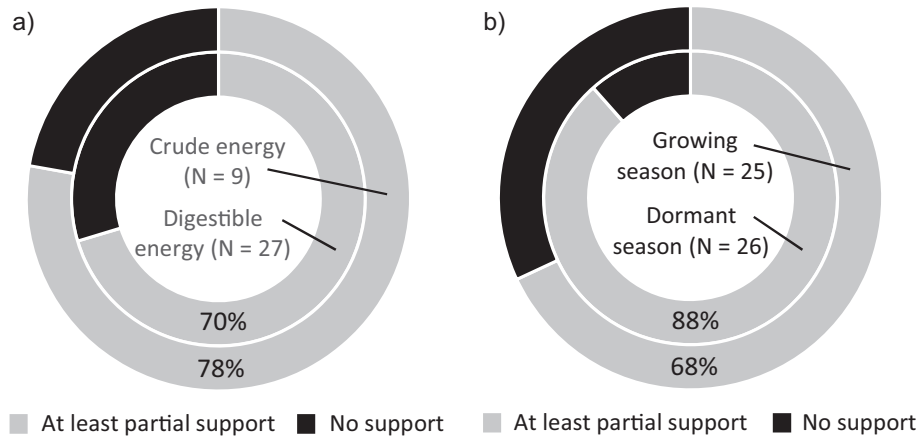


Fig. 2. The influence of (a) the way energy was measured or (b) study season on the extent of reported support for energy being a nutritional driver behind food selection in northern cervids. Data from 42* papers from a systematic search in ISI Web of Science and Scopus, 2016 (see *Methods* for details on search term and definition of driver). Figure (a) includes studies reporting some measurement of total energy; figure (b) also includes studies reporting on specific energy-providing constituents. Note that crude energy includes a few studies using biomass as a proxy for gross energy and that digestible measures include a range of chemical and computational methods. *Six papers excluded in (a) because crude or digestible total energy could not be discerned. One paper excluded in (b) as authors did not state the study season. Some studies looked at both seasons, and therefore, sample sizes add to more than the number of papers in the systematic search.

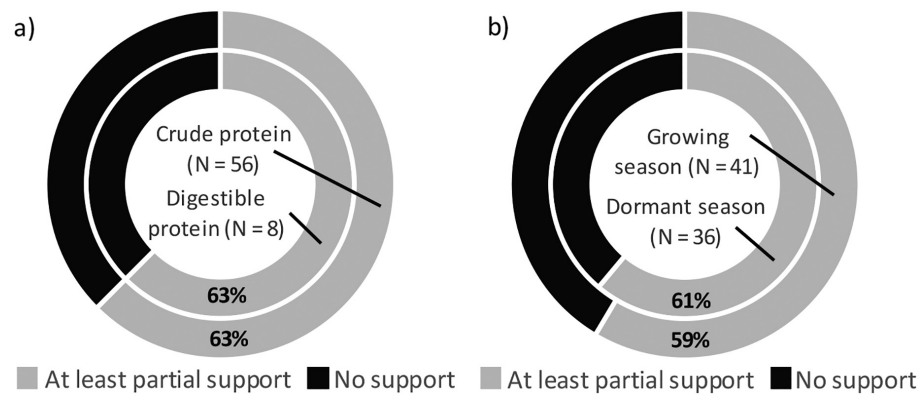


Fig. 3. The influence of (a) the way protein was measured or (b) study season on the extent of reported support for protein being a nutritional driver behind food selection in northern cervids. Data from 64 papers from a systematic search in ISI Web of Science and Scopus, 2016 (see *Methods* for details on search term and definition of driver). Some studies looked at both seasons, and therefore, sample sizes add to more than the number of papers in the systematic search. Note that digestible measures include a range of chemical and computational methods.

the role of energy and/or protein in food selection. The majority of studies gave support for these food constituents being positive nutritional drivers (Fig. 4). None of the studies reported a uniform negative influence of total energy or protein on food selection (but see partly such findings regarding protein and specific carbohydrates in Tixier et al. 1997, Verheyden-Tixier et al. 2008, McCusker et al. 2011, Ceacero et al. 2012). Note that support in our review for energy and protein being a driver of food selection not necessarily is support for the maximization hypotheses. We have deemed cases to be “positive support” where energy or protein was the food constituent or one of the food constituents

that most strongly explained food selection. This includes cases where other food constituents had an indiscernibly strong influence.

The frequency of support clearly depended on whether the studies measured both energy and protein (32 of the 74 studies did so, of which 20 additionally assessed one or more other food constituents). We found positive support in the far majority of studies that measured only energy or only protein, while the support became more nuanced and more complicated when we instead looked at the papers measuring more than one food constituent (frequency of positive support then dropped from 86% to 68% for energy and from 80% to 59% for protein; Fig. 4).

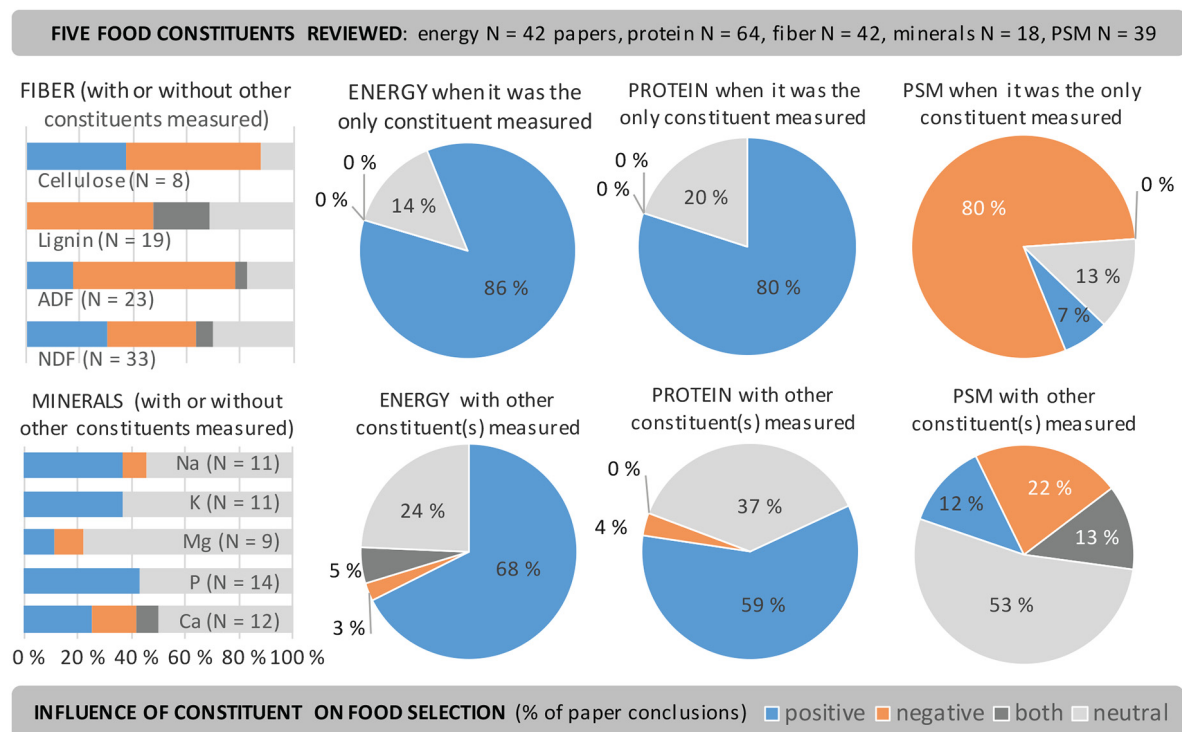


Fig. 4. The extent of reported support for various food constituents being a nutritional driver behind food selection in northern cervids. Data from 98 empirical studies from a systematic search in ISI Web of Science and Scopus, 2016. A positive or negative influence means that the driving role of the constituent was reported to be stronger or equally strong compared to other constituents measured. This includes partial such support, which are outcomes varying between, for example, season, animal category (e.g., sex or size), or in the case of energy and PSM, between constituent subgroups. Only food constituents with sample size ≥ 5 papers are shown. Proportions in the figure should not be interpreted as indicating the general strength of role as a nutritional driver for a given constituent relative to other constituents (such complex conclusions cannot be drawn by comparing results across vastly different study designs). PSM, plant secondary metabolites; NDF, neutral detergent fiber; ADF, acid detergent fiber.

Evidence from studies of selection among food types with different energy and protein contents.—Several papers of selection among food types revealed how food constituents co-vary, making it challenging and even impossible to tease apart the influence of single constituents. For example, in a feeding experiment with red deer, the most preferred of two plant options contained both higher nitrogen and higher non-protein cell contents and also had higher digestibility (Freudenberger et al. 1994). Macronutrients may also interact with plant secondary metabolites, which is illustrated by a similar experiment: Captive deer preferred plants with the highest content of energy when phenolic contents did not differ much between plants, but when differences in content of phenolics were high, the deer instead preferred the plants with the least phenolics despite these plants having less energy (McArthur et al. 1993). This highlights how studies looking only at energy or only at protein (or any single constituent) may produce erroneous conclusions. It also became clear that the much-studied tendency of cervids to select plants grown under more fertile conditions (Mereszszak et al. 1981, Danell et al. 1991, but see also Burney and Jacobs 2011) is consistently challenging to assign to protein or energy selection. Fertilization is commonly associated with higher nitrogen concentrations in the plant, but also bigger bites (Niemela and Danell 1988) and, thus, potentially higher energy intake (and also potentially less PSM; Stolter 2008).

Our review showed that we might gain knowledge about nutritional drivers even though the food types ingested are not identifiable (circumstantial evidence; Table 1). For example, habitat selection across several spatial scales by red deer in the Alps had a strong positive correlation with protein content of the available food (Zweifel-Schielly et al. 2009). Wapiti have been observed to be more mobile in order to feed more selectively in spring and autumn when food quality (author defined quality as more protein and energy) is higher compared to in winter (McCorquodale 1993). Such quantity–quality trade-offs that this selectivity implies are particularly evident in studies with a phenology context. For example, animals may not choose to feed in the most recent snowmelts, which have the most nutrient-rich vegetation, but instead feed in older

snow melts with higher biomass to obtain higher overall intake of nutrients (Van der Wal et al. 2000, Hebblewhite et al. 2008). The literature relating the effects of plant phenology to the foraging of migrating animals is vast (Avgar et al. 2014), but it is hardly possible to disentangle protein from energy in these data sets as they almost always stem from remote sensing (but see Hebblewhite et al. 2008).

The evidence above indicates the important role energy and protein play in food selection by northern cervids. Nevertheless, the question remains regarding the extent to which cervids maximize the intake of these food constituents, or regulate them to a certain target level. This question can only be addressed by studies including intake rates.

Evidence from studies of energy and protein intake.—The main approach for assessing the importance of energy-providing macronutrients on food choice has historically been the optimal foraging theory (OFT; Emlen 1966, Schoener 1971, Pyke et al. 1977). Well-known examples of such studies with northern cervids are the seminal papers by Belovsky (1978, 1984), where he concluded that moose in the summer selected food based on energy maximization. Notably, the finding was not based on direct observations of foraging moose, but on data inferred from food intake by an unknown number of individuals for an uncertain period. Belovsky later provided similar support for energy maximization by mule deer, white-tailed deer, and wapiti (Belovsky 1986).

Several of our review papers, however, point toward regulation toward a certain energy and/or protein target rather than daily maximization. This is not unexpected, especially for energy, given that ingestion of too much non-structural carbohydrates causes rumen pH to decline, potentially causing health issues such as ruminal acidosis (Wobeser and Runge 1975). By observing the food intake by separate groups of animals fed diets differing in energy density, Weber and Thompson (1998; fallow deer) and Webster et al. (2000; red deer) showed that deer ingested similar amounts of MJ/day regardless of diet group. In other words, the energy concentration of the food dictated how much (or how little) of the food they would eat.

Similarly, moose given free access to pellets of varying macronutrient concentrations did not

maximize daily energy intake, but instead mixed the pellet types consumed so that they reached a particular daily balance between protein and non-protein macronutrients (Felton et al. 2016, i.e., nutrient balancing, as discussed in a separate section below). When the moose were restricted in their choice of pellets, they ate such amounts that they consistently approached their daily target for energy from soluble carbohydrates, allowing their protein intake to fluctuate more. In a study by Asher et al. (2011), groups of lactating red deer receiving pellets varying in energy and protein content increased their daily dry matter intake to achieve the same intake of energy, which caused their protein intake to fluctuate.

A pattern of energy regulation is also indicated by mule deer having higher intake rates of low-starch than of high-starch pellets fed ad libitum, despite protein contents being higher (and fiber contents being lower) in the high-starch pellets (McCusker et al. 2011). When supplementing white-tailed deer with energy dense food, Schmitz (1990) and Timmons et al. (2010) found that deer continued to eat poor-quality browse instead of rejecting such in favor of higher-quality food items as predicted by OFT, a result that indicates that energy intake was not maximized, but regulated by the deer. The necessity to keep a ceiling on energy intake may also be influenced by the composition of soluble carbohydrates in the food, as, for example, sucrose and starch likely have different effects on the rumen environment (Eriksson et al. 2004). The socially most dominant red deer in Ceacero et al. (2012) acquired food with higher contents of total energy (through starch, fat, and NDF), but simultaneously lower contents of "sugar." In contrast, after closely observing the daily food intake of three enclosed red deer hinds feeding in natural habitats, Verheyden-Tixier et al. (2008) concluded that the availability of water-soluble carbohydrates, rather than proteins, tannins, and lignin, was the most important determinant of food selection. This positive influence of soluble carbohydrates is consistent with their results from a food selection study on roe deer (Tixier et al. 1997). As illustrated by these examples, it would be valuable if future studies addressing energy selection provide specific measures of carbohydrates, as per their functional role in the animal body.

Our review indicates that the northern cervids may also be regulating their protein intake. For example, fallow deer have been found to adjust their protein intake to match a certain target rather than maximizing it (Putman 1980), and moose to regulate toward a target balance between protein and non-protein macronutrients (Felton et al. 2016). Further examples are three experiments by Berteaux et al. (1998), Langvatn and Hanley (1993), and Asher et al. (2011), which rejected protein maximization in white-tailed deer and red deer, respectively. The Langvatn and Hanley (1993) study also compared protein and energy and found that protein intake rather than energy intake best explained how grazing red deer allocated their feeding time between grazing patches.

Intake rate measurements using natural forages were scarce in our review. Practically all of the studies with intake rates used manufactured or cultivated food, likely because this makes it easier to experiment with the nutritional contents of available food items. A common drawback with such food is that their protein content often exceeds the animals' needs, and if so, precludes a test of protein regulation to certain targets (the animals' protein need is met anyway). This may produce a biased view on the general importance of energy compared to protein as nutritional drivers. Apart from Verheyden-Tixier et al. (2008) mentioned above, the remaining studies using natural forages found protein to be an equally or more important driver than the other food constituents measured. For example, intake rates of native browse by tamed white-tailed deer in Koerth and Stuth (1991) could not be statistically attributed any more or less to protein than to structural fiber (energy was not measured).

That energy and protein interact as nutritional drivers in a complex manner is clear from the above synthesis of the literature. Fiber and tannins further confound the driving roles of protein and energy, and these two groups of constituents have therefore received particular attention in nutritional ecology (DeGabriel et al. 2014). Fiber is sometimes used to adjust the digestible energy of manufactured feed in feeding trials (Gray and Servello 1995), which can make it impossible to tease apart whether the animals are regulating their fiber or energy intake. Both fiber and tannins potentially reduce protein digestibility.

Because their effects are dose-dependent, we may study these issues most precisely with intake rates. Only one of the 19 papers measuring protein intake rates looked also at tannins (Verheyden-Tixier et al. 2008), while 10 looked at fiber. No consistent selection patterns emerged across the papers measuring protein and tannins or fiber. They used vastly different study systems, and most did not explicitly address the confounding aspect of fiber versus tannins reducing protein digestibility. For example, sika deer increased their intake rates when fed oak browse compared to agricultural silage, apparently circumventing the browse's reduced digestibility in order to achieve a protein target (energy was not measured; Kim et al. 1996). However, the reduced digestibility of browse could also be due to more tannins (not measured) rather than only more fiber (measured). Clearly, there is a need for more studies on the subject.

The influence of season on selection for energy and protein.—Protein and energy concentrations in the diets of northern cervids generally peak during the growing season, broadly following plant phenology (Leslie et al. 1984, Meyer et al. 1984, Kucera 1997, Abbas et al. 2013). Because of this strong influence of phenology, it seems natural to postulate that the selection for energy and protein in food should vary with season. As Parker et al. (2009, p. 57) fittingly state, “The deposition and mobilization of body fat and body protein vary... as species use dietary income and body stores to integrate the profits of summer and the demands of winter.”

Nonetheless, our review shows that there is insufficient empirical evidence to say that cervids select more strongly for protein in summer than they do in winter. Only nine out of 64 papers measuring protein in our review actually investigated whether protein selection varies between these seasons for a given study system. Furthermore, we found that all the nine papers either negated such a pattern (Gillingham et al. 2001, Barancekova et al. 2007) or gave only partial support for it (Tixier et al. 1997, Moser et al. 2006, Verheyden-Tixier et al. 2008, Zweifel-Schielly et al. 2009, 2012, Dostaler et al. 2011, Miranda et al. 2012), varying, for example, between demographic groups or for only parts of either season. Only two studies tried to compare the relative seasonal role of protein versus energy

(McCorquodale 1993, Gillingham et al. 2001), which are too few to generalize from. Looking at the influence of season across all our review papers (note: not within the same study), we found that the reported support for protein being a nutritional driver was similar in the growing season as it was in the dormant season (Fig. 3b), while for energy such support was reported more often for the dormant season than for the growing season (Fig. 2b). Of the 42 papers measuring energy, 26% had investigated food selection in both the dormant and the growing season.

Our literature search did not include many studies addressing the influence of body size and sex on energy or protein selection. Contrary to expectation from theory, tame individuals of the small-bodied mule deer selected a winter diet that had lower energy content than was selected by the larger-bodied red deer (Hobbs et al. 1983), possibly due to rapid ingestion and excretion (see also Schweiger et al. 2015). With regard to the influence of sex, some studies reported that females have a higher protein intake or selection for protein than males (Staines et al. 1982, Padmalal and Takatsuki 1994, Miranda et al. 2012) or that there were no differences between the sexes (Weckerly and Nelson 1990, Jiang et al. 2009).

Summary of energy and protein as drivers of food selection.—Our review revealed a high frequency of support for both protein and energy being influential drivers of foods selection by northern cervids. In the 32 papers measuring both food constituents, we found no evidence that the intake of one consistently takes priority over intake of another. Indeed, the likelihood for reporting a neutral conclusion (energy or protein having neither a clear positive nor a negative driving influence) increases, it seems, when more than one constituent is measured (Fig. 4). This reflects the complexity of synergistic and antagonistic interactions among these (and other) constituents, and the complexity of the animals' continuous response to physiological feedbacks while selecting their food (Simpson and Raubenheimer 2012). In our review, the apparent strategy of many study animals was that of regulating to a certain energy and/or protein target level rather than maximization. One final important finding was that there is insufficient

empirical evidence for the notion that cervids more strongly select for protein in summer than they do in winter.

Nutritional strategy (3): regulation or limitation of dietary fiber?

Background: why should cervids regulate or limit fiber in their diet?—Dietary fiber is an ambiguously used term that typically describes the structural carbohydrates of plant cell walls, mainly hemicellulose, cellulose, and lignin. The symbiosis with rumen microbes enables ruminants to ferment hemicellulose and cellulose for energy, while lignin is considered indigestible (Van Soest 1994). Hemicellulose is considered more fermentable than cellulose, yet requires a longer retention time than non-structural carbohydrates (Van Soest 1994). Fiber can also increase handling time (cropping, chewing, and rumination; Shipley and Spalinger 1992, Perez-Barberia and Gordon 1998). However, we must not forget that cellulose and hemicellulose are the main fuel for ruminants, typically providing up to 80% of their energy (Barboza et al. 2008).

Fiber also provides structure for the rumen microbes, which affect digestion of not only the fiber itself, but also other food constituents (Tomkins et al. 1991). The rumen microflora adapt to different types of forage, and altered digestion times can increase the tolerance or need for more fiber (Gordon et al. 2002). Because of this intricate feedback loop, it has been postulated that the need to regulate fiber is a necessary nutritional strategy for ruminants (Jones 1972, Van Soest 1994).

Here, we summarize findings of 42 empirical papers from our systematic search that address the role of various fiber fractions in food selection. Given that these fractions are functioning differently in the animal body, we report the results separately for each fraction measured. The most common method used to analyze fiber contents is the detergent analysis (Van Soest et al. 1991, Van Soest 1994). This approach divides the fiber into the two technical fractions neutral detergent fiber (NDF) and acid detergent fiber (ADF), and also acid detergent lignin (ADL, which may include minor traces of bound nitrogen or ash). Fiber is sometimes categorized into the functional fractions hemicellulose (NDF–ADF), cellulose

(ADF–ADL), and lignin (ADL). If available, we made interpretations based on the three functional measures, because they contain no merger of digestible and indigestible fractions, which NDF and ADF do.

If we combine all fiber fractions, nearly half (44%) of the conclusions from the papers showed negative association between fiber and food selection. If we separate fiber fractions, the picture becomes more intricate (Fig. 4), and several studies showed positive or partially positive (context-dependent) associations. In contrast to what we found for the other food constituents, all the 42 fiber studies assessed one or more food constituents besides fiber. When placing the varying influence of different fiber fractions into such multi-constituent contexts, we clearly saw the importance of having study designs that capture sufficient variation in the contents of food constituents.

Evidence of fiber regulation from studies of selection among food types.—Almost half of the 27 selection studies of fiber looked only at NDF or ADF or crude fiber; that is, they did not distinguish digestible and indigestible fractions. It is difficult to interpret nutritional drivers from studies reporting only crude fiber. Interpreting studies reporting some, but not all three technical fractions from the detergent analysis is also tricky. A negative association between food selection and ADF content, for example, is likely avoidance of its indigestible portion of lignin, not avoidance of the more beneficial cellulose (as indicated in Danell et al. 1994, Dumont et al. 2005, Stewart et al. 2011). A series of such studies addressing fiber and twig bite size illustrates well also the confounding issue of co-variation with other food constituents: Fiber content generally increases and digestibility decreases with bite size, but concentration of secondary metabolites that possibly inhibit digestibility may also decrease (Palo et al. 1992). An apparent selection by moose for larger twigs (with higher NDF or ADF) may in part be a trade-off to avoid phenols or tannins (Jia et al. 1997, Stolter et al. 2005).

Studies that test hemicellulose, cellulose, and/or lignin directly are easier to interpret, and there were eight such studies among the fiber selection papers. Zweifel-Schielly et al. (2012) showed that forest-dwelling red deer selected food to obtain higher concentration of hemicellulose, but lower

concentration of lignin, as expected from the digestive functions of the different fractions. However, digestible fiber fractions may also be negatively associated with food selection, as shown for cellulose and red deer on natural lands in New Zealand (Forsyth et al. 2005, Bee et al. 2011), and roe deer during spring in France (Tixier et al. 1997).

Evidence of fiber regulation from food intake.— There were 13 studies measuring fiber intake rates among our review papers. None of these reported digestible functional fractions directly (four measured lignin), and only three distinguished between digestible and indigestible technical fractions. Several of these studies are examples of correlations between fiber and other food constituents, where it is difficult to elicit which nutrient is driving food choice. In another case, where protein concentrations varied among the available food, fallow deer grazing in cultivated monocultures had higher intake rates of the protein-rich white clover than of the fiber-rich fescue (Piasentier et al. 2007). A cafeteria trial with white-tailed deer on Anticosti Island during winter showed that secondary metabolites may impede interpretation about fiber: Deer strongly preferred balsam fir over white spruce, but the preference was negatively correlated with

both high NDF and high levels of condensed tannins (lignin, protein, or phenols did not differ between the plant species; Sauve and Cote 2007).

The influence of season on fiber selection.— Because of its strong effects on digestion (net energy return), the influence of fiber on food selection is expected to depend on seasonal energy needs (Miranda et al. 2012). Only six out of the 42 fiber review papers had data from the same animal–food system in more than one season, and we could deduct no clear pattern from these. Lignin and ADF were the only fiber fractions with a near-consistent association with food selection within a season (negative respectively in the dormant; and in the growing season, Fig. 5). This may reflect a general seasonal difference in the lignin portion of ADF.

Verheyden-Tixier et al. (2008) is a comprehensive example showing this seasonal trade-off also with other food constituents: When water-soluble carbohydrates and protein were equally available in grasses and browse during summer, red deer selected for browse (as indicated by the proportion of their daily dry matter intake), despite its higher contents of lignin and tannins. However, in winter, when grasses had more water-soluble carbohydrates than deciduous browse, red deer switched to grazing mode, resulting in a lower lignin intake, but a higher

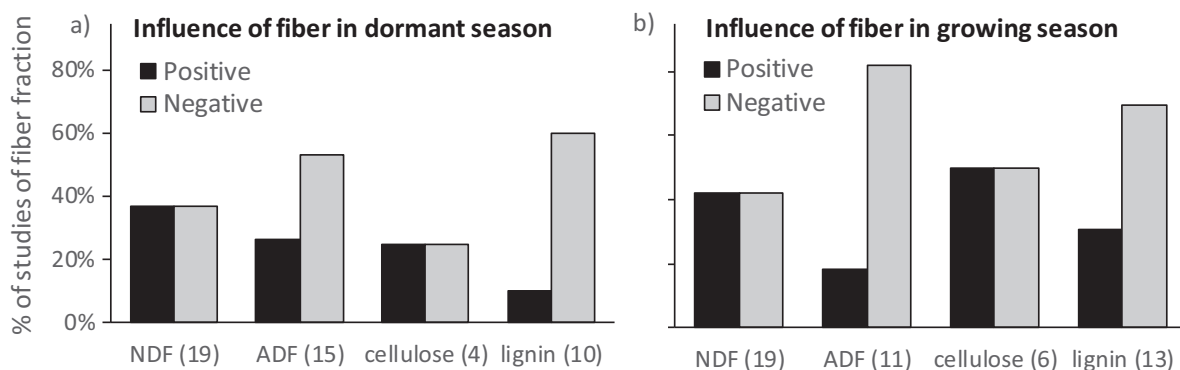


Fig. 5. Prevalence of least partial association between fiber content of food and food selection of northern cervids in (a) the dormant and (b) the growing season. Review of 42 papers from a systematic search in ISI Web of Science and Scopus, 2016. Numbers after fiber fractions on x-axes denote the number of studies of that fraction in the given season; for example, 15 of the 42 papers measured ADF in the dormant season, of which 27% reported positive and 53% reported negative association (20% reported no association, which is not shown in the figure). Hemicellulose is not included due to low sample size ($N = 2$ in each season). Because the same study could show both positive and negative support (depending on, e.g., animal category), percentages within a fraction and season may sum to more than 100%. NDF, neutral detergent fiber; ADF, acid detergent fiber.

intake of digestible fiber. Red deer in the Swiss Alps selected for a diet lower in lignin and higher in hemicellulose than expected from availability, and more strongly so in spring than in autumn (Zweifel-Schielly et al. 2012). This may reflect higher needs for energy after winter depletion. As such, in this review we found many examples (Figs. 4, 5) that negate the common notion that high fiber equals low diet quality for northern cervids.

Summary of fiber as driver of food selection.—There were many relevant papers linking food selection to food contents of fiber in our review. However, incoherent use and reporting of chemical analyses hampered our ability to draw knowledge from them about nutritional drivers. Two patterns appear consistent, however: (1) The literature does not support the common notion that high fiber necessarily equals low diet quality for northern cervids; and (2) northern cervids appear less inclined to avoid fiber during winter than during summer. We stress the advantages of focusing on the functional fractions (hemicellulose, cellulose, and lignin) rather than the technical fractions (NDF and ADF), as these tell quite different stories (Fig. 4). The need to address co-variation with other food constituents also became particularly evident in our fiber review. In future studies, ruminants' trade-offs between different fiber functions should be treated as a regulating process, including trade-offs with other constituents, rather than an issue of selecting for high digestibility.

Nutritional strategy (4): regulation or limitation of minerals?

Background: why should cervids regulate or limit minerals in their diet?—Minerals are inorganic elements that are essential to life due to their role in maintaining practically all physiological functions (Robbins 1994). This importance is clearly demonstrated by their influence on the spatial distribution of large herbivores (McNaughton 1988, Freeland and Choquenot 1990). Seven macrominerals (Ca, P, Na, Cl, K, Mg, S) and seven trace minerals (Co, Cu, I, Fe, Mn, Se, and Zn) are considered essential under normal conditions (NRC 2007). The individual requirements of different minerals vary with animal species, sex, season, and life stage (for cervids, see

Pletscher 1987, Weckerly and Nelson 1990, Grace and Wilson 2002, Ceacero et al. 2010). However, essential minerals are rarely available in natural food items in a composition that matches the animals' needs (Ohlson and Staaland 2001). The use of non-food resources to satisfy mineral requirements (e.g., by geophagy or the utilization of mineral licks; Pletscher 1987, Heikkila and Harkonen 1998, Ayotte et al. 2008) indicates that the intake of minerals by cervids is not always linked to plant selection.

Evidence of mineral regulation (studies with all types of inquiry).—Most studies in our systematic search dealt with variation in the mineral content of food plants and/or whether a certain diet met an animal's mineral needs, without linking this to food selection. Only 19 papers fit into one of our defined types of inquiry. All papers measuring a trace mineral also measured at least one macromineral. In ten of the 11 studies of mineral selection among food types, researchers included at least one macronutrient constituent (most often protein), but seldom used statistical approaches to look for interactions.

Fraser et al. (1980) observed seasonal and sex differences in the frequency of moose's utilization of feeding sites with aquatic plants: Males used such sites more frequently than females in early summer, which in part could be related to mineral contents of the available plants. Sodium has been quoted as the mineral of interest in this study (as in Belovsky 1978, 1984), although other minerals (Ca, Fe) were also higher in the most utilized areas. Notably, sodium was not the mineral most frequently found in our review papers (which was calcium and phosphorous; Fig. 4).

All the papers looking at mineral intake rates (N = 3) dealt with only minerals, and two of the three studied the animals' intake of minerals from manufactured mineral salts, not from plant material (Ceacero et al. 2009, 2010). Although such mineral sources do not reflect natural sources, they may provide valuable insights into animals' ability to discriminate between different minerals and whether requirements are mirrored by feeding choice (Ceacero et al. 2009, 2010).

We could not draw any general patterns of mineral selection, given the low number of studies and the many minerals most of them addressed. The prevalence of neutral associations (Fig. 4) was unexpected, but likely reflects the

fact that many of these studies were not designed to investigate food selection, and especially not the complex co-variations among minerals or between minerals and other constituents. In plants, minerals are often complex bound. For example, glucosinolates are a group of PSM with sulfur being part of the functional group. Therefore, an animal's avoidance of food with high contents of the mineral sulfur (Ceacero et al. 2015) might also be related to the deterrent effect of PSM. Minerals are also known to interact with macronutrients and even gastrointestinal parasites (Freeland et al. 1985, Parkins and Holmes 1989, Ram et al. 1998, Spears 2003, Campbell and Hewitt 2004). Complexity is further added by interactions among minerals within the animal's body (e.g., competition for absorption sites), resulting in the need for a balanced intake (Ram et al. 1998, Spears 2003). Simple correlation tests or rankings, which were common in the mineral studies in our review, may not be statistically sufficient to separate all these confounding factors.

Ceacero et al. (2015) found a strong negative influence of sulfur content on plant selection by red deer in natural settings. The authors suggest that the mineral functioned as the main driver of the observed food selection and that its dose-dependent toxicity might drive the deer's overall nutritional strategy (i.e., regulation or limitation of minerals; Robbins 1994). We do not know whether cervids are generally able to detect toxic levels of minerals. However, red deer can discriminate between different minerals (Ceacero et al. 2010), so cervids should be able to select minerals to some extent and according to their particular needs. Nonetheless, potentially toxic heavy metals are frequently found in animals and must have been ingested, for example, cadmium in liver (Aastrup et al. 2000, Jarzyńska and Falandysz 2011).

Summary of minerals as drivers of food selection.—The most obvious finding of our review of these mineral papers was the lack of patterns for specific minerals, and a tendency overall for neutral associations. We need both more advanced statistical analyses and more empirical data to tease apart the complexity in natural settings of (1) co-variation among minerals and between minerals and other food constituents, (2) the various roles of minerals in metabolic

synergies and antagonistic relationships, and (3) the trade-offs facing a foraging animal because there are so many essential, but also potentially toxic minerals.

Nutritional strategy (5): avoidance or regulation of plant secondary metabolites?

Background: why should cervids avoid or regulate PSM in their diet?—In their defense against herbivory, plants have evolved a myriad of different plant secondary metabolites (PSM; Iason et al. 2012), varying, for example, with plant ontogenetic stage (Boege and Marquis 2005, Wam et al. 2017), seasonality, and site conditions (Stolter et al. 2010, 2013). Since the first papers addressing the interaction between PSM and animal food selection were published (Freeland and Janzen 1974, Bryant et al. 1980, Robbins et al. 1987), these compounds have been generally assumed to have negative effects on mammal health and fitness. PSM can nutritionally limit animals either by restricting diet diversity or the amount of a single plant type that can be eaten or by reducing nutrient absorption (Robbins et al. 1987, Iason 2005). The physiological effects of PSM largely depend on dosage (Villalba et al. 2002). However, studies about the actual effects of PSM on the physiology of cervids are rare (Iason 2005). In recent years, PSM (mainly tannins) have also been shown to have some beneficial effects on the animal (Hoskin et al. 2000, Makkar 2003), depending on, for example, season (Chapman et al. 2010).

The variety in composition and concentration of PSM is higher in trees, herbs, and forbs (which are all dicots) than in monocotyledonous grasses (Mithofer and Boland 2012). Therefore, browsers have more strongly developed physiological counter-adaptations than grazers, for example, in mucoproteins in the saliva, rumen bypass, liver size, or rumen symbionts (Shipley 1999, Shipley et al. 1999, Makkar 2003, Goel et al. 2005), described as the tolerance continuum (Iason and Villalba 2006).

Evidence of PSM avoidance or regulation (studies with all types of inquiry).—In our literature review, we found 39 papers addressing PSM that were applicable to one of our three types of inquiry. While there were few positive associations, negative associations were as prevalent as neutral

associations (depending on whether other constituents were measured; Fig. 4). A few studies showed a positive or a partially positive association between PSM contents and food selection (e.g., Zweifel-Schielly et al. (2012) on red deer, Tixier et al. (1997) on roe deer, and Stolter (2008) on moose), which means that animals were not deterred by high concentrations of PSM in their food.

Most of the studies of selection among food types also measured other food constituents (22 out of 28 papers), but only two out of ten studies with intake rates did so. The PSM papers generally focused on three PSM groups: tannins, phenolics, and terpenoids, while other groups were practically absent (there was one study of alkaloids). Only eight of the papers dealt with more than one PSM group. Given that most dicots contain multiple groups of PSM, there may be effects of unknown compounds that were not addressed in these studies. We did not find a consistent pattern of the reported association with food selection for any PSM group. We postulate two main explanations for this ambiguity: (1) High variety of PSM composition in the plants creates a multi-dimensional feeding environment for herbivores (Villalba et al. 2002) that seemed to be not sufficiently taken into account in many of the studies. (2) There was a lack of analyses of more specific PSM compounds. PSM are still being pooled into very coarse groups for analysis without knowing their actual bioactivity, even though we have become aware of the different effects of specific compounds.

While many studies reported total phenolics, which includes the tannin fractions (i.e., polyphenols) in the plant material (e.g., by the method of Folin-Ciocalteu), others addressed more specific phenolic groups such as low molecular weight phenolics (e.g., Sunnerheimsjöberg and Hamalainen 1992). Stolter et al. (2005) have shown a higher importance of specific phenolics for moose food selection compared to condensed tannins. Looking only at tannins in a study may therefore render quite different conclusions than looking at total phenolics. Even condensed tannins are a mixed group, and a recent study shows that subgroups of tannins may influence moose food selection differently (Wam et al. 2018). As a typical browser, moose particularly face seasonal variation in food types. Studies of

free-ranging moose in northern Sweden show a clear negative influence of specific low molecular weight phenolics on food selection on willows in winter, yet stronger influences of other compounds (and morphology) in summer (Stolter et al. 2005, 2013).

The tannin studies in our review most frequently reported neutral associations with food selection. Only two of the studies described a clear negative association (Sauve and Cote 2007, Bergvall 2009). The remaining negative associations depended on, for example, the reproductive status of the animal, spatial arrangement of feeds, season, and diet composition. Most of these studies measured intake rates and were conducted with animals in captivity using manufactured tannins not naturally available in northern plants, such as single specific tannins (tannic acid) or the mixture quebracho (but see, e.g., Sauve and Cote 2007, Chapman et al. 2009). The partial avoidance observed in these tannin studies may therefore be a result of non-familiarity rather than an adapted nutritional strategy applicable to the species in natural settings (Rautio et al. 2007).

Our review papers showed negative associations varying with the chemical structure of terpenoids (e.g., different effects of mono- or diterpenes on food selection (Tixier et al. 1997)), or tree size and age (Vourc'h et al. 2001, Burney and Jacobs 2011). Only one study (Beck and Peek 2005a, wapiti and mule deer) assessed the role of alkaloids. It found a negative association. At northern latitudes, alkaloids are mostly found in herbaceous plants, and seldom in woody plants (Handeland 2008). Herbaceous plants seem generally less investigated in studies of food selection by northern cervids, which may be one reason for the lack of alkaloid studies, and another reason may be the well-known high toxicity of these PSM, which therefore may have the highest priority as drivers of food selection.

Summary of plant secondary metabolites as drivers of food selection.—In our review of the influence of PSM on cervid food selection, negative or partly negative associations were as prevalent as neutral associations. Our review highlighted possible explanations for the ambiguous findings (points 1–2 above). We need to incorporate more fully this knowledge in future PSM studies, not the least in our use of statistical modeling

approaches. This becomes particularly challenging if the goal is to look at interactions between PSM and other food constituents (Stolter et al. 2005, 2013). When designing our studies, we must remember that PSM compositions in the foodscapes of animals are not in a steady state, but differ with vegetation succession, seasons, climate, and more.

Nutritional strategy (6): nutrient balancing?

Why should cervids balance food constituents in their diet?—Nutritional ecology is a complex matter, as the sections above clearly show. Westoby (1974) suggested it already in the 1970s, and it is becoming increasingly clear, that foraging should be seen as a dynamic, multidimensional process which involves balancing the intake of many different food constituents to satisfy complex nutritional needs that change over short timescales (Simpson and Raubenheimer 2012). What is a suitable food in the morning is not necessarily the best choice in the afternoon. The need to take a multidimensional approach is reflected by the pool of observations showing how important mixed diets can be for ungulates (Westoby 1974, Oldemeyer et al. 1977, Rogers et al. 1980, Schmitz 1990, Parsons et al. 1994, Berteaux et al. 1998, Beck and Peek 2005b, Hanley et al. 2014). We suggest that many of the inconsistencies we have seen among studies of the same taxa in the sections above are due to such dynamic processes. The nutritional state of an individual actually changes with each consecutive meal. What is a perfect food choice at one point in time (at which we may infer a certain nutritional strategy) is not suitable at another point in time (at which we may infer another strategy). The following discussion about the role of nutrient balancing in cervid food selection is less systematic than the previous sections, because of an almost complete lack of targeted studies into nutritional balancing of cervids. Instead, it should be seen as a reflection for further research.

Despite the inherent complexity, evidence for nutrient balancing has been found in a wide variety of taxonomic groups globally, including herbivores, omnivores, and carnivores (Simpson et al. 2004, Raubenheimer et al. 2005, Robbins et al. 2007, Dussutour et al. 2010, Erlenbach et al. 2014), and spanning a wide range of spatial and

temporal scales. The animals have been found to alter their food intake on a daily or near-daily basis to achieve a specific nutritional target balance in the diet. They do this either by selecting nutritionally balanced food types or by combining food types with compositions complimentary to each other. Behind this regulatory feat are several neural and chemical processes and feedbacks operating before, during, and after digestion (see, e.g., Provenza 1995, Berteaux et al. 1998, Lindsley and Rutter 2004, Yarmolinsky et al. 2009). Many studies of nutrient balancing have used the Geometric Framework for nutrition (GF), an analytical framework which can empirically deal with several nutritional currencies at the same time (Simpson and Raubenheimer 2012).

With access to detailed data on intake of specific food constituents by individuals given free access to a wide variety of food options, one can also use geometric models to identify the animals' intake target—the amount and balance of nutrients that is optimal for them given the physiological state they are in at the time (Raubenheimer and Simpson 1997). However, because animals cannot allocate 100% of a nutrient ingested to useful purposes, the intake target also comprises the constrained losses (Simpson and Raubenheimer 2012). The intake target of captive moose winter time has been identified in an experiment where individuals mixed their daily food intake (pellets) in such a way so they reached a particular amount and balance between macronutrients every day (Felton et al. 2016). To identify the nutritional balance of free-ranging animals is of course much trickier than using captive individuals. What is needed to conduct such studies is detailed animal observations under suitable conditions (Hjeljord et al. 1990, Weckerly 1994, Nordengren and Ball 2005). Even though sample sizes would presumably be small, such observations of wild individuals would be highly valuable. Because the nutritional state of an individual changes with each consecutive meal, we must design these intake rate studies so that they encompass full-day observations of focal individuals. Identification of diet compositions in a large number of rumen samples (not as much influenced by digestion as feces) may also reveal patterns of food constituent intake on a population level.

If an animal only has access to non-complementary nutritionally imbalanced foods, it will not be able to reach its intake target. The animal's response in this circumstance is known as a rule of compromise, because it shows which compromise the animal makes between overeating the constituent in high concentration against undereating the constituent in low concentration (Felton et al. 2009b, Rothman et al. 2011). To study the rule of compromise is one way of illustrating how consumers must make trade-offs due to the fact that food constituents are available for consumption in the form of food packages, not in isolation. When restricted to either of two nutrient-rich but imbalanced pelleted diets, all the moose in the experiment mentioned above maintained a relatively stable intake of non-protein energy (carbohydrates and fats) while allowing protein intakes to vary with food composition (Felton et al. 2016). In other words, even if the different age–sex classes may have had different target proportions (e.g., calves' target balance had a higher protein:non-protein ratio than adults' target balance), they expressed the same rule of compromise. Further studies with more individuals and a larger number of different diets are needed to confirm those results. In natural settings, one can identify such prioritizations forced upon the animals by changing seasons or altered competition (Felton et al. 2009b). By understanding the rule of compromise of free-ranging animals, food intake can be predicted, as can potential repercussions of changes in management (Raubenheimer and Simpson 2006).

CONCLUSIONS

This review of the nutritional drivers behind food selection of northern cervids was guided by six established hypotheses in nutritional ecology. Despite extensive research interest in the foraging and nutritional strategies of large herbivores (901 papers deemed potentially relevant in our systematic search), only 98 papers (11%) actually link food selection with data on the nutritional contents of the food. No study in our systematic search looked at all five constituents reviewed (energy, protein, fiber, minerals, and PSM), and several of the papers looked only at one (33%) or two (37%) food constituents. Our review shows that the outcome of assessments that take several

constituents into account conveys a more complex story than assessments that only focus on a single constituent, no matter which constituent is in focus (Fig. 4), reflecting a high degree of co-variation and interaction. The basic nutritional and physiological knowledge necessary for analyzing how these interactions influence or confound our assessments of herbivore food selection remains incomplete. Interesting topics for further research may be to assess how frequently and in what ways the digestible fractions of macronutrients are correlated with each other in the plant material eaten by the northern browsers, and how correlations between crude protein and PSM affect the variation of digestible protein and resultant intake rates.

What is most important perhaps is that we have illustrated the large variety of influences that a given food constituent appears to play in the food selection of these animals. Our review provides wildlife ecologists with a guiding framework for current research needs:

1. We encourage researchers into herbivore nutritional ecology to consider food constituents in synchrony, by assessing how animals trade off linked benefits or costs of several food constituents, not just a main few. This approach can shed light on the functional roles of different constituents, the basic nutritional strategy of the animals, and their nutritional priorities in times of scarcity. Using the Geometric Framework for nutrition (GF) is one promising approach. Irrespectively of approach, however, we must take into account co-variation between food constituents, as they are available to animals only as food packages. A focus on only one or a few constituents may tell only a portion of the underlying complex, dynamic patterns of the animals' nutritional strategy. It is also important to note that we currently lack sufficient biological knowledge to address adequately diet selection, even when we apply the GF approach. For example, more research is needed regarding the processes underlying the herbivores' tolerance for certain PSM and how this influences food selection. All such knowledge can then be linked to other important variables influencing herbivore food selection.

2. The findings in our review influence our view on what constitutes food quality. They clarify that the value of a particular food to the feeding animal is not a fixed property, but frequently changes with time and circumstance as the sought-after food constituent(s) may change with each consecutive meal. We suggest that some food items which conventionally would be classified as being of low quality may for some herbivores be of high quality at certain times, due to the combination of food constituents and structures they contain. Many of the studies in our review looked only at parts of the diet, for example, only some of the food types composing the diet at a given time. That particular part may not reflect the overall driving role of a food constituent as animals may use certain food types to regulate their intake of certain food constituents. Studies therefore need to capture a large proportion of the food types contributing to the diet and sufficient variation in available and used nutritional contents.
3. There is a lack of research into the intake rates of food constituents by free-ranging cervids, which we need in order to understand the nutritional priorities and compromises of the animals, with regard to food availability, food processing and toxin tolerance, etc. Because intake rates from captive studies are difficult to extrapolate to wild populations (DeGabriel et al. 2014), we encourage the development of techniques that facilitate collection of intake rates in the wild. One potential pathway is the use of drones and advanced collar cameras. Because the nutritional state of an individual changes with each consecutive meal, we must design these intake rate studies so that they encompass full-day observations of focal individuals.
4. By lumping several food constituents or their functional fractions into composite measures such as energy, fiber, ash, or tannins, we may mask their respective functions. We cannot emphasize enough the importance of conducting chemical assays that allow one to quantify the proper fraction of a food constituent and its actual availability to the animal in question.
5. Our findings clearly call for more research on seasonal differences in the nutritional strategies of northern cervids. Some patterns emerged in the review papers: The cervids appear to avoid lignin less strongly during winter than during summer. In addition, our review revealed a lack of empirical evidence for saying that cervids more strongly select for protein in summer than they do in winter. We caution that this may be one of ecology's "illusory truths" until more studies actually compare data from several seasons within the same study system.

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