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Review Article

Trophic Flexibility: Herbivores Navigating the Green and Fungal Worlds

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Abstract

The diet of wild North American ungulates has traditionally been categorized as herbivorous, with the inclusion of fungi considered an anomalous phenomenon. Recent studies challenge this notion, revealing the significant presence of mushrooms in cervids' diets, particularly during the fall season. The peak of mushroom consumption in autumn is attributed to the increased energy requirements of animals approaching winter Replace with [1-3] and the heightened availability of mushrooms from July to November Replace with [4], [2]. Selecting fungi as a supplementary dietary component is unsurprising, given the high nutrient content of mushrooms, making them an ideal addition to the diet of ungulates attempting to stockpile energy when access to lush forbs diminishes [5]. Moreover, research indicates that fungal spores remain unaffected by the ruminant digestive tract Replace with [6-8]. In essence, cervids act as vectors, dispersing fungal spores into the environment, enabling fungi to colonize areas otherwise inaccessible Replace with [9]. This underexplored mutualistic relationship between wild ungulates and fungi sheds new light on trophic interactions in forested habitats.

Key Words: Trophic flexibility; Herbivores ; Fungal consumption; Seasonal dietary variation; Reproductive females; Caloric intake; Nutritional breakdown; Moisture content; Trophic considerations; Ecological implications

Abbreviation: Non-Protein Nitrogen (NPN); Volatile Fatty Acids (VFAs)

Introduction

It is well established that many small mammals in north American forested regions play a part in ecosystem nutrient cycling through the consumption of fungal fruiting bodies [10]. These enticing and often nutrient-dense dietary additions, known as sporocarps, have been documented as significant food items for various species [8]. However, when it comes to larger mammals, such as the numerous cervid species in North America, fungi are often understated, relegated to being considered a mere bonus food item. Despite both historical and contemporary research documenting the seasonal importance of fungi, especially in fall diets, their significance is frequently downplayed [11]. Whether cervids consume fungi to meet basal metabolic requirements during periods of high energy expenditure, to condition their bodies for the upcoming breeding season, or to accumulate vitamins and minerals found in limited quantities in plant matter, it is evident that there is a purpose behind the seasonality of mushroom consumption.

Fungi consumption serves as a means to an end for wild ungulates, but the repercussions of such interactions extend beyond the individual's health. Many fungi rely on mycophagist animals for spore dissemination [12], and would struggle to colonize new areas independently. For instance, *Hypogeous fungi*, developing their fruiting sporocarps underground, lack the means for spore release through water or aerial transportation unless unearthed by a mycophagist [8]. Through dietary selection, cervid species may influence the diversity and success of fungi species in a region, subsequently impacting fungal associations and inoculum available to plant species [13]. In this way, mycophagists play a role in shaping the landscapes they inhabit through trophic interactions.

This article delves into the existing literature on mycophagy in mammals, focusing specifically on wild ungulates, aiming to elucidate both the drivers and consequences of cervid mycophagy. By examining the relationships between animals, fungi, and their ecosystems, we can gain a deeper understanding of the significance of these trophic communications. The review's objectives include determining the reasons for the seasonal significance of fungi in cervid diets, analyzing the nutritional value of fungi, and exploring the far-reaching effects of mutualistic relationships between fungi and cervids on the ecosystems they inhabit.

Drivers for Selection of Fungi in Diet

The foundation of wild ungulate dietary preferences lies in the intricate interplay of various factors steering their selection towards fungi [14]. This pivotal section explores the fundamental drivers shaping the inclusion of mushrooms in the diets of these animals. As we embark on this journey, our exploration unfolds through two distinct lenses: the temporal dynamics encapsulated in "Seasonal Dietary Variation" and the unique nutritional demands, especially pertaining to energy acquisition, faced by "Reproductive Females and Caloric Intake." Each heading within this section unravels a different facet of the nuanced relationship between ungulates and fungi, offering insights into the seasonal patterns and reproductive imperatives that guide their dietary choices. By dissecting these drivers, we aim to establish a comprehensive understanding of the intricate factors steering the dietary preferences of wild ungulates.

Seasonal Dietary Variation

Research indicates that deer selectively consume mushrooms in significant quantities primarily during the fall months [3], typically ranging from no earlier than July to near the end of November [4]. Several theories attempt to explain this behavior. One hypothesis suggests that the peak in mushroom production during the fall, facilitated by moist and mild weather conditions, makes fungi more readily available, driving their inclusion in the diet [15]. However, the fall season is characterized by ungulates seeking to consume more than required by their basal metabolic needs, as they strive to increase fat reserves for the impending harsh winter [3]. Given the heightened caloric requirements during this period, it is logical for ungulates to incorporate alternative dietary items such as fungi to fulfill these nutritional needs.

Reproductive Females and Caloric Intake

Specifically in the case of reproductive females, additional caloric intake during the fall is of even greater importance [16]. Females possess a smaller digestive tract coupled with a higher metabolic rate than adult males, making them less efficient at processing high-fiber or high-cellulose diets [17]. Moreover, females face more severe consequences if ill-prepared for winter compared to their adult male counterparts [18]. Ungulate females must acquire sufficient energy reserves to support not only their own requirements but also to provide sustenance to growing fetuses during gestation and later during lactation [16]. The addition of fungi to the diet can provide nutrient-dense and highly digestible energy, assisting reproductive females in conditioning their bodies for successful reproduction. Previous studies examining the reproductive success of reindeer (Rangifer tarandus) populations in Finnish Lapland have highlighted the critical role fungi play in the success of ungulates, from implantation to reproductive maturity [19]. In years where mushroom growth was insufficient, female reindeer struggled to maintain adequate weight going into the breeding season, leading to delayed calving dates in the spring and decreased average birthweight of offspring [19]. This trend was visible even in years where a lengthened thermal growing season allowed for greater consumption of plant matter, but other factors had inhibited fungal growth. This study emphasized the importance of a productive mushroom harvest for reproductive success, underscoring the significant role fungi play throughout the reproductive process of ungulates.

Quantifying Fungal Consumption

Understanding the intricacies of ungulate dietary choices requires an exploration of the driving forces behind the selection of fungi in their diets[20]. This section delves into the multifaceted factors influencing the dietary preferences of wild ungulates, focusing on the seasonal dynamics observed in their mushroom consumption. The examination begins with an analysis of the seasonal dietary variations, shedding light on the specific timeframes when fungi play a pivotal role in their nutritional intake. Additionally, we delve into the nuanced nutritional needs of reproductive females, elucidating how caloric considerations during the fall season become of paramount importance for sustaining both the individual and the growing offspring. By dissecting these drivers for the selection of fungi, we aim to unravel the intricate relationships between ungulates and their fungal dietary components.

Nutritional Breakdown of Fungi

For both male and female cervids, recent studies have unveiled that mushrooms constitute a more significant portion of the diet than previously perceived [13]. Earlier perspectives tended to categorize mushrooms as a supplementary food item, preferred by ungulates but not comprising a substantial portion of the diet [15]. However, recent research has shown that not only do fungi make up a substantial portion of the diet, in some cases, they are the largest proportion. In a study examining the dietary habits of white-tailed deer (*Odocoileus virginianus*) residing in white pine-hemlock forest habitats in Maine, gilled mushrooms were found to make up 45.2% of the fall diet, marking the largest dietary percentage for any given food item across all four seasons [3]. Another study focusing on white-tailed deer in a hardwood forest region of central New Hampshire revealed that mushrooms comprised the largest percentage, 27.5% of the dry weight consumed by deer in the fall, making it the most frequently eaten dietary subject during that season [21]. Further studies documented even greater fungi consumption by deer; in Alabama pine-hardwood forests, white-tailed deer were observed consuming 71.2% of their diets as mushrooms on a fresh weight basis [22]. Studies in Arizona found similarly high mushroom consumption for late summer/early fall mule deer (*Odocoileus hemionus*) diets, with findings that fungi made up 65.8% of the diet [23]. Mule deer in Montana also confirmed this trend, with mushrooms composing 59.9% of their August diets [24]. Analyzing the collective data from these studies clearly illustrates the critical role fungi play in the diets of cervid species across a variety of habitats.

Moisture Content

Fungi generally exhibit high water content, with an average moisture content ranging from 74% to 90% on a fresh weight basis. This elevated water content makes most fungi less nutrient-dense when freshly harvested compared to when dried. Consequently, larger quantities of fungi must be consumed to obtain nutritional benefits [15]. However, despite the lower nutrient density in freshly harvested fungi, water content has not been identified as a limiting factor in intake. Ruminants, including cervids, possess the ability to efficiently absorb water through the rumen [25].

Protein Content

Fungi exhibit a wide range of protein content depending on the species, with studies finding specimens ranging from as low as 4% to as high as 44% on a dry matter basis [26]. Despite this considerable variation, mushrooms are generally acknowledged as a valuable source of protein. In comparison, forbs and shrubs generally contain 8-22% crude protein and are typically 37-78% digestible, while fungi are approximately 58-91% digestible [17]. Moreover, research on the amino acid profile of fungi suggests that mushrooms contain a higher amino acid content compared to plants, with methionine acting as the limiting amino acid [27]. Additionally, mushrooms contain non-protein nitrogen (NPN) in the form of chitin, urea, and nucleic acids [26]. In ruminant animals, NPN is utilized by ruminal microbes to form ammonia, combined with carbon skeletons to form amino acids. These amino acids are then metabolized by ruminal microbes to create microbial protein, which can be digested by the ruminant. Compared to monogastric animals, ruminants can ferment and digest additional nutrients from fungi that would only be accessible through ruminal breakdown. It has been hypothesized that nitrogenous compounds in fungi may even be more digestible for ruminants than the NPN found in plants, given that fungal cell walls are composed of chitin rather than lignin [15].

Carbohydrates and Cell Structure

Approximately half of the dry matter of mushrooms is composed of carbohydrates, with mycorrhizal species noted to contain higher sugar concentration than saprotrophic species [27]. A diverse array of compounds makes up the nonstructural carbohydrates in fungi, with the main structures being pentoses, methyl pentoses, hexoses, disaccharides, amino sugars, sugar acids, and sugar alcohols [15]. Polysaccharides found in fungi include glycogen, which plays a role similar to starch in plants by acting as an energy storage compound [26]. This is unusual, considering that glycogen is typically found in animal tissue, while starch and cellulose are seen in plant matter [27]. Other carbohydrates found in fungi include oligosaccharides such as mannitol and trehalose. Trehalose, in particular, is a common occurrence in fungi and has earned itself the colloquial title of "mushroom sugar" [26]. Trehalose is present in greatest quantities in young specimens and is converted to glucose as the mushroom matures.

The carbohydrates found in fungi serve an additional purpose beyond providing a basic energy source to ruminants; they also aid in the digestion and utilization of other feedstuff. The digestion of structural carbohydrates in fungi induces the rumen to produce greater amounts of volatile fatty acids (VFAs), allowing for greater digestibility of other higher fiber forages. This is likely due to the need for branched-chained VFAs by fibrolytic bacteria to synthesize amino acids and long-chain fatty acids [28]. In studies evaluating cellulose digestion in sheep, it was found that the digestibility of low-protein hay was markedly improved when VFAs were added to the diet [29]. Subsequent studies evaluating fiber digestion in cattle further corroborated this pattern [28]. Trials evaluating cellulose digestion in cattle showed that when fed diets containing different forages, digestibility of the forages was positively impacted by the supplementation of VFAs into the diet in 15 out of 16 occasions. Research examining the diets of white-tailed deer in central Maine found that during the fall, when mushrooms were plentiful, digestibility of dried leaves was greater due to being consumed alongside fungi [3]. This positive impact on digestion is critical for deer given their small rumen volume and high metabolic needs [30]. It would not be feasible for diets to be composed of large amounts of high-fiber forage without the addition of items such as fungi, which allow for enhanced digestibility.

Vitamin and Mineral Profile

The vitamin and mineral content of fungi species varies widely depending on the richness of the substrate they are grown in [31]. On average, the mineral content in fungi is higher than that in fish and meat and nearly twice that found in most vegetables [32]. The most commonly seen vitamin derivatives found in fungi include ascorbic acid, niacin, riboflavin, biotin, and thiamine [26]. For ruminant animals, these vitamins serve little purpose due to the innate ability of ruminants to produce their own vitamin C and vitamin B through digestive processes [33].

The mineral breakdown of fungi, however, provides a valuable resource to ruminants [34]. Fungi accumulate high concentrations of various minerals critical to cervids (Launchbaugh and Urness [15]). Fungi are particularly high in minerals such as potassium and phosphorus, with some studies finding potassium concentrations to be 20 to 40-fold higher in fungi fruiting bodies than concentrations found in the soil they were grown in [27]. Both potassium and phosphorus content in fungi exceed the maintenance requirements for weaned ungulates, offering a valuable source of minerals [15]. While plant matter typically has high calcium levels but insufficient phosphorus, fungi have an inverted calcium to phosphorus ratio. This allows ungulates to source critical minerals from fungi that would otherwise be challenging to obtain from forage alone. Fungi also accumulate high concentrations of selenium, which is particularly useful in areas where the soil concentration of selenium is low, such as the Olympic Peninsula region of Washington state [35]. Selenium deficiency can lead to dire consequences such as white muscle disease in cervids, making adequate intake of this mineral of great importance.

Ecological Implications

As we delve into the dietary habits of wild ungulates, the significance of their fungal consumption extends far beyond individual nutritional choices. In this crucial section, we navigate the broader implications that arise at the intersection of animals and fungi within ecosystems. "Ecological Implications" explores the intricate dance between ungulates and fungi, unraveling the mutualistic relationships that contribute to the ecological tapestry. The examination begins with a focus on "Animal and Fungal Relationships," shedding light on the symbiotic connections forged through spore dispersal and dietary choices. Extending our exploration, we then delve into "Trophic Considerations," elucidating the secondary effects rippling through ecosystems as a consequence of fungal consumption. This section aims to provide a holistic understanding of how the dietary habits of wild ungulates reverberate throughout the natural world, shaping landscapes, plant communities, and trophic dynamics.

Animal and Fungal Relationships

Once the significance of fungi in the diets of wild cervids has been acknowledged, the next crucial step is to examine whether the relationship between cervids and fungi is mutualistic [13]. While there is a wide array of obvious benefits for cervid populations, it's essential to explore what fungi gain or lose from these interactions. For many fungal species, the key to survival and procreation lies in their ability to disperse spores. Methods of spore dispersal may range from utilizing vectors such as water or air, active ejection, to dispersal via animals [36]. Previous research has established that epigeous fungal species rely more heavily on spore dispersion via air or water, with animal dispersion only being incidental, while hypogeous and mycorrhizal fungi have a greater need for animal interference [37], [8].

For species that have a greater dependency on mycophagists, fungi often use methods to attract mammal species, such as the production of a strong aroma when their fruiting bodies have matured. This odor allows fungal foragers to locate mushrooms with greater ease, similar to how a flower would attract a pollinator. Once consumed, fungal spores are not broken down during digestive processes and may later be deposited in novel areas yet to be inhabited by fungal colonies [38], [8]. Deer species are markedly beneficial for this purpose. Unlike smaller mammals, deer travel longer distances and aid in spreading spores over a larger habitat area, thus diversifying fungal colonies throughout their home range. Additionally, when mycophagist animals are consumed by predators, fungal spores can maintain their structure even through a second round of digestion and are transported to new locations [13]. These interactions further demonstrate the mutualistic relationship between ungulates and fungi.

Trophic Considerations

Beyond the primary interactions between animals and fungi alone, their connections lead to secondary ripple effects throughout the ecosystems they inhabit. Previous studies have examined the consequences of extracting mycophagists from their native landscapes and found that their absence impacted plant communities as well as fungal communities [13]. In western Australia, one study found that when an enclosed habitat area was compared to an open area where mycophagists were able to roam freely, it was noted that the enclosed habitat had four times as much arbuscular mycorrhizal fungi as the open habitat area. In the open area, ectomycorrhizal hypogeous species were more common, likely due to mycophagist selection for their larger fruiting sporocarps, which serve as a higher nutritional quality food source [39]. When soil from each enclosure was used to inoculate native plant seedlings, those inoculated with soil from the open area had far greater biomass than the enclosed area [13]. This difference is understood to be due to the beneficial plant host associations of the ectomycorrhizal fungi, which been produced as a result of selective dietary habits of mycophagists.

Soil perturbation by foraging mycophagists was noted to be a driving factor in creating aerated soils and decreasing the risk of wildfire in specific forested areas of Australia [13]. When mycophagists were present, bioturbation was found to increase water absorption and lead to higher rates of organic decomposition in foraged areas by breaking up hydrophobic soil layers and creating micro catchments. When mycophagist species faced extensive predation and suffered decreased numbers in Australia, the subsequent desertification of many previously forested regions was identified as being caused largely in part by the decreased bioturbation [13]. However, it is essential to note that the relationship between the presence of mycophagists and wildfire/desertification risk in North American forested regions remains unconfirmed.

Future Research Directions

The consumption of fungi by wild ungulates extends beyond individual dietary preferences, giving rise to profound ecological implications that resonate throughout their habitats. In this section, we unravel the intricate relationships between animals and fungi, delving into the mutualistic interactions that define their coexistence. The examination begins with an exploration of the symbiotic ties between ungulates and fungi, shedding light on how the foraging behaviors of these animals contribute to the dispersal of fungal spores and the shaping of fungal landscapes. From this primary interaction, we extend our gaze to trophic considerations, exploring the ripple effects that emanate throughout ecosystems. As we dissect the trophic connections between animals and fungi, we uncover secondary consequences that reverberate through plant communities, soil structures, and even wildfire risk. Through a comprehensive lens, this section aims to elucidate the broader ecological implications of fungal consumption by wild ungulates.

Determining Fungal Species:

Many previous studies examining dietary choice of cervids have only referred to fungi in general terms and sought to determine the inclusion of any fungi in the diet. Future research highlighting the specific species of fungi being consumed would be useful for exploring the frequency and proportion of consumption, determining the nutritional breakdown of each species, and examining the potential drivers for selection of certain species over another. Previous methods that were able to successfully classify species of fungi consumed utilized research methods such as assessing fecal samples from wild deer[17] or observing food selection by tame deer [3], [23]. For future research, it would be beneficial to use both strategies in combination by allowing tame deer to roam a study area and collect fecal samples which then could be analyzed using DNA barcoding techniques. The benefit to utilizing both strategies would be that researchers would be able to observe foraging strategies by the deer as well as collect concrete data from the fecal analysis. DNA barcoding would be advantageous over observation alone because through the act of amplifying fungal DNA via polymerase chain reaction researchers would be able to determine fungal species without the need for spores or visible structures [17]. This technique could also be employed by using rumen content samples collected from wild deer carcasses brought in by hunters, a tactic which has been used in previous studies [40], though not before used in conjunction with DNA barcoding.

Exploring Circadian Rhythms and Reproductive Cycles

While our current research focuses on the dietary habits of ungulates, particularly their consumption of mushrooms and the ecological implications thereof, an intriguing avenue for future investigation lies in the potential interplay between these dietary behaviors and circadian rhythms governing estrus and rut cycles. The notion that ungulates may exhibit specific feeding patterns in alignment with circadian rhythms adds a layer of complexity to our understanding of their adaptive responses to environmental changes.

Considering the well-established link between circadian rhythms and reproductive cycles in various species [41, 42], it is conceivable that the seasonal variations in mushroom consumption observed in our study may be intricately connected to reproductive strategies. The circadian regulation of hormonal fluctuations could influence not only the timing of reproductive events but also the dietary preferences of ungulates [43, 44].

As researchers delve into the chronobiology of these animals, investigating how their foraging behaviors align with the natural cycles of their environments may uncover novel insights into the adaptive responses of populations. Furthermore, recognizing the potential population-specific adaptations in diverse environments could open avenues for targeted studies on the interplay between environmental factors, circadian rhythms, and reproductive success.

While our current study lays the groundwork for understanding the dietary choices of ungulates and their ecological impact, the integration of chronobiological perspectives could pave the way for a more comprehensive exploration of the intricate relationships between these fascinating animals and their environments.

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Conflict of Interest

There are no conflicts of interest involving this article.

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