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The effect of Red Deer browsing pressure on the subsequent selection of bilberry plants by Red Deer and Lepidoptera Larvae

Effekten av hjortebeiting på blåbærplanter for seleksjon hos hjort og Lepidoptera larver

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Preface

This thesis was written as the final paper of my master program in Natural Resource Management at the Norwegian University of Life Sciences. This process has given me a lot of insight and experience with field work, statistics and scientific writing.

I want to express my gratitude to my two supervisors Dr. Stein Joar Hegland and Professor Stein Ragnar Moe for their wonderful help, advices and support throughout this period. I also want to thank Katrine Eldegard for helping me with the statistics. This thesis is part of The EcoDynDeer project (Ecological dynamics caused by red deer herbivory), sponsored by The Research Council of Norway and Sogn og Fjordane University College, in collaboration with the Norwegian Red Deer Center. I want to thank Johan Trygve Solheim and the Norwegian deer center for the opportunity to be a part of this project, as well as their hospitality. Last but not least, I want to thank my lovely friend and assistant Sofia Sjøblom for her constant support, optimism, constructive criticism and help throughout this undertaking.

Abstract

Browsing by deer may induce defence in plants which may subsequent affect food quality for herbivores. Lepidoptera larvae are thought to be more sensitive to defence substances in plants than larger herbivores, like red deer, because of a simpler digestion system. This study focus on how previous browsing pressure by red deer, affected selection of bilberry plants by red deer and Lepidoptera larvae. Cafeteria trials were used to study bilberry preference by Lepidoptera larvae and red deer. Bilberry with four different browsing histories was presented to larvae and deer: unbrowsed, lightly browsed, moderately browsed, and highly browsed. Both larvae and deer avoided the heavily browsed bilberry which represented an artificial high level of deer densities. Larvae preferred lightly browsed plants, while the results indicated that deer preferred the moderately browsed plants. I conclude that larger herbivores do not show a strong selection against previously browsed bilberry plants. Lepidoptera larvae did avoid previously intensively browsed plants and were more selective in food choice.

Hjortbeiting kan indusere forsvar i planter, som igjen kan påvirke hvordan herbivorer selekterer planter. Lepidoptera larver antas å være mer sensitive for forsvarsstoffer i planter enn større herbivorer som hjort, på grunn av et enklere fordøyelsessystem. Denne studien undersøker hvordan tidligere hjortebeiting på blåbærplanter påvirker hjortens og Lepidoptera larvenes beitepreferanser. Kafeteriatester ble brukt for å studere blåbærpreferanse hos larver og hjort. Blåbær med fire forskjellige beitehistorikker ble presentert for larver og hjort: ubeita, lett beita, moderat beita, og hardt beita. Både larver og hjort unngikk hardt beita blåbærplanter som representerte en kunstig høy hjorttetthet. Larver foretrakk lett beita planter, mens mine resultater tyder på at hjort foretrakk moderat beita planter. Jeg konkluderer med at store herbivore ikke viste noen sterk seleksjon mot tidligere beitede blåbærplanter. Lepidoptera larver unngår tidligere hardt beita planter og var mer selektive i sine valg av planter.

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Introduction

Deer is a keystone species (Côté et al. 2004; Rooney and Waller 2003; Waller and Alverson 1997) because they directly influence growth, reproduction and survival of plants through selective feeding (Côté et al. 2004; Waller and Alverson 1997). Deer have been reported to supress the regeneration of favoured tree- and other palatable species (Côté et al. 2004; Knight et al. 2009; Pigott 1983; Putman et al. 1989), as well as species sensitive to herbivores (Côté et al. 2004; Putman et al. 1989; Waller and Alverson 1997). Consequently, deer may improve conditions for less favoured species (Pigott 1983; Waller and Alverson 1997), and species that are more tolerant to herbivory (Côté et al. 2004; Putman et al. 1989).

Plants have a wide variety of defence mechanisms (Côté et al. 2004). However, plant defence is costly and may affect the nutrient availability in plants (Stamp 2003). The Growth-Differentiation Balance (GDB) hypothesis proposes that there is a trade-off between allocating resources for growth, or defence, in a system with limited amount of resources available for the plants (Herms and Mattson 1992; Stamp 2003). In environments without herbivores undefended plant usually performed better than defended plants (Gómez and Zamora 2002). Timing and intensity of herbivory, plant genotype, growth strategies, history and past defoliation, density of competitors, and to what degree a plant is under nutrient or moisture stress, are all factors that influence plant performance, see more in Côté et al. (2004).

There are several theories of how plants respond to browsing. Plants may invest in regrowth with low amount of defence substances, or allocate resources for defence and less for regrowth, or plants may allocate resources in equal amount for regrowth and defence (Meijden et al. 1988).

Plant response to herbivory may be positive for herbivores when plants respond by increased vegetative production (Bergqvist et al. 2003; Makhabu et al. 2006; Price 1991; Stamp 2003), because such plant tissue are commonly rich in nutrients, and low in defence substances (Volenec et al. 1996; White 1978). Browsing may lead to less competition among the surviving shoots, and benefit the plant (Du Toit et al. 1990).

An increase in nutrients available in regrowing tissue has been an explanation for the continuing feeding of plants with previous browsing history (Heichel and Turner 1983; Volenec et al. 1996; White 1978). Belsky et al. (1993) proposed that compensatory growth is a general strategy in response to any type of damage a plant is subjected to, and not specifically to damage by herbivores. Tolerance may be a preferred response if the damage is minimal, and regrowth is more economical compared to the cost of producing defence substances (Belsky et al. 1993; Herms and Mattson 1992). The specific response of a plant may be determined by the resources available, and the cost of producing defence (Belsky et al. 1993).

The effect of browsing may be negative for herbivores if plants respond by producing defence substances (Bryant et al. 1994; Duncan et al. 1998). Defence substances can reduce palatability, have an effect on the digestive system, or they could be toxic (Bryant et al. 1992; Hjeljord 2008). Often the defence substances will have all three properties (Bryant et al. 1992). The changes in nutrient availability in the plant due to browsing, may affect other herbivores preference for the plant (Pedersen et al. 2011). How herbivores react to these defence substances depend on the species digestive system (Ayres et al. 1997).

Ruminants have several compartments with microorganisms to catalyse digestion (Schmidt-Nielsen 1997), and the more complex digestion system of ruminant animals, like deer, is presumably less affected by defence substances in plants, compared to non-ruminant herbivores (Meisingset 2008). In addition, white tailed deer (*Odocoileus virginianus*) have tannin-binding proteins in their saliva that bind the normally toxic and digestive inhibitory tannins (a defence substance) in to none toxic compounds that pass through the digestive system without affecting digestibility (Austin et al. 1989). Robbins et al. (1987) reported that white tailed deer suffered no effects of tannins, which have been reported for domestic sheep.

Although insect digestion is simpler than that of mammalian herbivores, insect digestion varies a lot between species and specialisations (Wolfson and Murdock 1990). How well species are able to utilize plants, depends on the enzymes present in the gut and how they are compartmentalized (e.g. some insects can utilize plants that other herbivores find highly toxic) (Terra et al. 1996). Defence substances may influence insect herbivory differently, depending on plant-insect interactions and on the herbivore digestive capabilities (Ayres et al. 1997). Pöykkö et al. (2005) found that experimentally removing certain defence substances increased the survival of larvae on Lichens, and in the subsequent preference test, larvae chose the plants with experimentally reduced defence substances.

In this study I investigated Lepidoptera larvae (*Lepidoptera sp*) and red deer (*Cervus elaphus*) selection of bilberry (*Vaccinium myrtillus*) subjected to four different browsing intensities.

Cafeteria trials were used to assess larvae and deer first choice of plants, and larvae leaf consumption. I hypothesised that previous intensive browsing pressure would increase defence substances in bilberry plants, resulting in reduced palatability. Less browsed plants will subsequently be preferred over more intensively browsed plants. I expect that the effect of previous browsing will be stronger in Lepidoptera larvae than in deer, because deer has a more complex digestive system than larvae.

Method

Study Site

The experiments took place in the summer 2014 at the Norwegian red deer center in Svanøy. Svanøy is an island in Flora municipality (6857539.188N,-26580.5E) in western Norway. Svanøy has a temperate costal climate with mild winters and warm summers. Precipitation normally varies between 1500- 3000 mm a year, and temperature average 1-2 ^{o}C in February, and 14 ^{o}C in August (Dannevig 2009). The terrain on the island is rugged and reaches a summit of approximately 300 masl. The landscape is mostly dominated by Scots Pine (*Pinus sylvestris*), while the understory is mostly dominated by bilberry. Patches of other forest types, cultivated fields and mires do also exist. No forestry activities have been carried out in the last decades, and the wild red deer population is large throughout the island, and likely to be representative for the deer densities in western Norway (J.T. Solheim; S.J. Hegland, personal communication, 2014).

Study Species

Bilberry is a deciduous dwarf shrub and presumed to be relative herbivore tolerant (Dahlgren et al. 2007; Hegland et al. 2010), although contradictory responses to browsing have been observed (Dahlgren et al. 2007; Hegland et al. 2005). It is suggested that bilberry recovery from browsing, depends on the amount of damage inflicted and where the damage occurred (Tolvanen et al. 1992).

Red deer are ruminants (Hjeljord 2008; Meisingset 2008) and classified as intermediate browsers (Hjeljord 2008; Latham et al. 1999; Meisingset 2008), were diet changes depending on the season (Hjeljord 2008). Bilberry is the main winter food for deer in Norway (Melis et al. 2006), but it is not a highly preferred plant by red deer (Hegland et al. 2013; Mysterud et al. 2010). Deer populations in Norway have increased substantially since the 1960s (Mysterud et al. 2010; Statistisk sentralbyrå 2014).

Lepidoptera is an order of insects that includes moths and butterflies (Schmidt-Nielsen 1997). Herbivorous species have adapted to feed on every part of the plant, some may even utilize plants other herbivores find toxic (Terra et al. 1996). All Lepidoptera larvae used in this study was captured on bilberry.

Bilberry Collection

The bilberry used in the experiments was collected from different sites in Svanøy, and divided into four categories based on the previous browsing pressure history: unbrowsed, lightly browsed, moderately browsed and highly browsed. Unbrowsed plants were collected from deer exclosures. These plants had not been browsed for a minimum of 13 years. Although the exclosure prevented deer from entering, it did not prevent other animals such as rodents, birds and invertebrates. Any sign of previous browsing on plants collected within the exclosures were considered browsed by other animals, and excluded from the experiment. Plants with light and moderate browsing intensities were collected from sites outside the exclosures and were categorized by the amount of browsing damage on the ramet. The damage was determined by the amount of damaged branches divided by the total amount of branches. Plants with damage from 10- 20% were categorized as lightly browsed intensity, and plants with browsing damage from 40- 50% where classified as moderately browsed intensity. Only plants with clear evidence of browsing were used for the lightly and moderately browsed categories. Highly browsed plants were collected from within a deer enclosure at the Norwegian red deer center and represented a deer population at artificially high density, beyond a natural carrying capacity because of supplementary feeding. These plants have been heavily browsed since 1993 (S.J. Hegland, personal communication, 2014). All plants were kept in jars with water for three days.

Cafeteria trials

Lepidoptera Larvae

This experiment used one leaf, from one plant, from each of the four categories. The leaf selected for the experiment was selected for its general size and healthy appearance. The size of the leaf was measured using millimeter paper, were the leaf size were the number of squares covered. If 50% or more of the square was covered, the square was counted. If the leaf covered less than 50% of an individual square, it was not counted. The leaf was measured before and after the trial. The difference in number of squares was used as an estimate of the amount of leaf tissue eaten. The leaves were measured by the same person before and after the trial, in order to minimize error.

Figure 1: Test cafeteria trial with larvae. One leaf form each of the four browsing intensities was given a random position, and a larva was placed in the middle in order to minimize influence on leaf choice.

Larvae was captured using sweep nets in a bilberry forest in Østmarka, (Lørenskog) Norway (6649298.219N, 276948.219E) and in Svanøy at the end of May 2014. The larvae could not be identified to species level, but were divided into different morph types based on their overall shape, size and colour. The larvae were kept in glass jars until they were used in the experiment.

Larvae preference in browsing intensity was tested in a petri dish with one leaf from each of the four browsing intensities. Filter paper was placed in the bottom and saturated with water to keep the environment humid for both larvae and leaves, subsequently minimize drought stress, and to keep the leaves fixed while the larva moved around. The position of each leaf was marked on the lid in numbers from 1 till 4. The larva was placed in the middle of the petri dish, making the distance to each leaf approximately equal, in order to minimize the influence of position on leaf choice. The larvae were observed the first 20 minutes to record first choice. First choice in this study was defined as “the first leaf the larvae or deer would begin eating”. After recording first choice, the larvae were left over night to eat. The experiments lasted 12 hours before the leaves were measured once more. The experiment was repeated 80 times with different larvae, over six days. All glass petri dishes were cleaned before the onset of each experiment.

Red Deer

The cafeteria trail for red deer took place in the beginning of August. Whole plants were placed in a frame and presented to deer inside an animal pen, were first choice was observed. The frame consisted of a lath that locked the plants in place at ground level. Two different strategies were used to record deer first choice: deer were released into the animal pen one by one, or all animals were released into the pen at the same time. This alteration was done to increase the number of first choice observations. If more than one deer approached the frame at the same time, they were pushed away.

Figure 2: The frame presented to deer with plants from the four different categories.

Statistical analysis

For the analyses of the cafeteria trials for larvae and deer, two circumstances were investigated: the consumption of leaf tissue by larvae, and the observed first choice made by both larvae and deer. All statistical analyses were performed using R (R Core Team 2014).

Leaf consumption

In order to analyse if previous browsing intensity influenced the proportion of leaf eaten by the larvae, we initially fitted a generalized linear mixed model (GLMM) with log-link function, assuming a Poisson distribution of errors, using the package lme4 (Bates et al. 2013). The response variable was 'the amount of leaf eaten'. Browsing intensity, with four levels: unbrowsed, lightly browsed, moderately browsed and highly browsed, was included as a fixed effect, with the unbrowsed category as reference level. The natural logarithm of the leaf size was included as an offset variable to control for the natural variation in leaf size. The location for collection of larvae was included to control for regional effects of preference. The experiment number nested in location was included as a random effect in the model to account for the repeated sampling at each location. Larvae morph type was included as a separate random effect to account for differences in preferences between morphs. The initial GLMM model was checked for over-dispersion by inspecting the generalised Pearson statistic, gPs = $\chi^2/(N\text{-}p)$, where N = number of observations and p = number of parameters (Crawley 2013).The model was highly over-dispersed gPs = 36.9. We suspected that this could be due to zero-inflation in the response variable (60.6 %), and thus re-fitted the model as a zero-inflated Poisson, using the glmmADMB package in R (Bolker et al. 2012), but this model did not converge. Next, we refitted the model as a negative binomial model using the glmmADMB package, but this model was substantially under-dispersed (gPs = 0.47). Finally, we decided to handle the over-dispersion in the initial model by adding an observation-level random intercept (Zuur 2013).

First choice

To test my prediction that larvae were more selective than deer in food choice a goodness of fit test and a Fisher test was used. The first choice of larvae and deer were analyzed separately with a goodness of fit test. A goodness of fit test compares the observed first choices for each browsing intensity to what is theoretically expected. A Monte Carlo approach was used in the EMT package (Menzel 2013). To compare whether there were a detectable difference in preference between deer and larvae first choice, a Fisher's Exact Test for Count Data was used. A chi square test could not be used due to the small sample size.

To test if the leaf seize may have influenced larvae first choice a multinomial logistic regression was used. However, as none of the larvae selected the highly browsed category as a first choice, the category could not be included in this test.

An exact binomial test was conducted to test whether larvae and deer did avoid the highly browsed category. We predicted that although there would be differences in first choice, both deer and larvae would avoid the highly intensively browsed bilberry. This test tested if the observed distribution deviated from the theoretical expected distribution for larvae and deer.

Results

Leaf consumption

In total, leaf consumption was recorded for 80 Lepidoptera larvae. Larvae consumed significantly more of the lightly browsed bilberry compared to the other browsing intensities (Table 1, Figure 1).

Table 1: The model of browsing intensity on larvae leaf consumption. Response variable was "the amount of leaf eaten". Only lightly browsed leaves were significantly more browsed than the other browsing intensities.

Explanatory variables	B	SE	z	P
Fixed effect				
Browsing intensity				
Intercept	-8.0412	0.8386	-9.589	<2e-16
Lightly	1.9506	0.8273	2.358	**0.0184**
Moderate	0.2739	0.8176	0.335	0.7376
Highly	-0.4930	0.7969	-0.619	0.5362
Random effects	Σ	SD	Number of obs	Number of groups
Location	9.569e-08		292	2
Experiment:Location	1.520e+01		292	73
Morph types			292	10
Observation-level random intercept			292	292

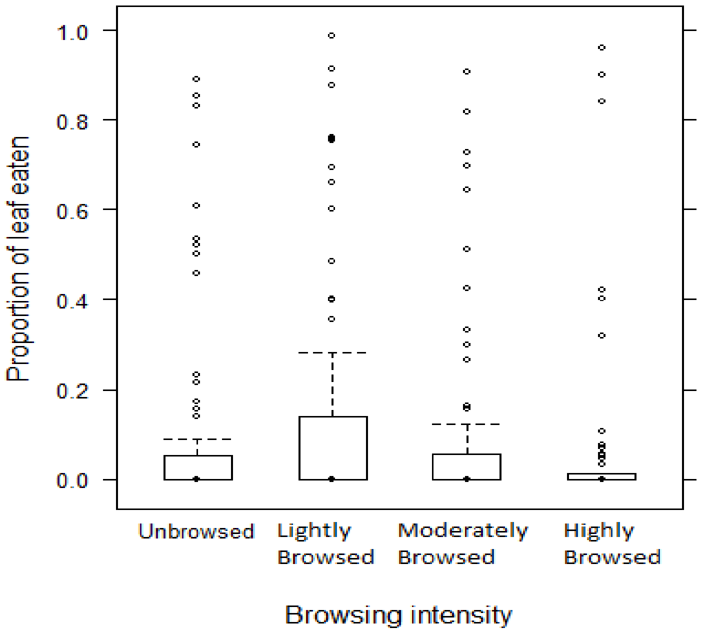

Figure 1: The observed proportion of leaf eaten in the four categories by Lepidoptera larvae with upper quartile, upper extremes and outliers.

First choice

Out of the total number of larvae, 20 larvae were also recorded on first choice along with 22 red deer. As their observed first choice, larvae chose the lightly browsed leaves most frequently, followed by the unbrowsed leaves. Deer chose the moderately browsed bilberry most frequently as their first choice, followed by lightly browsed and unbrowsed (Figure 1).

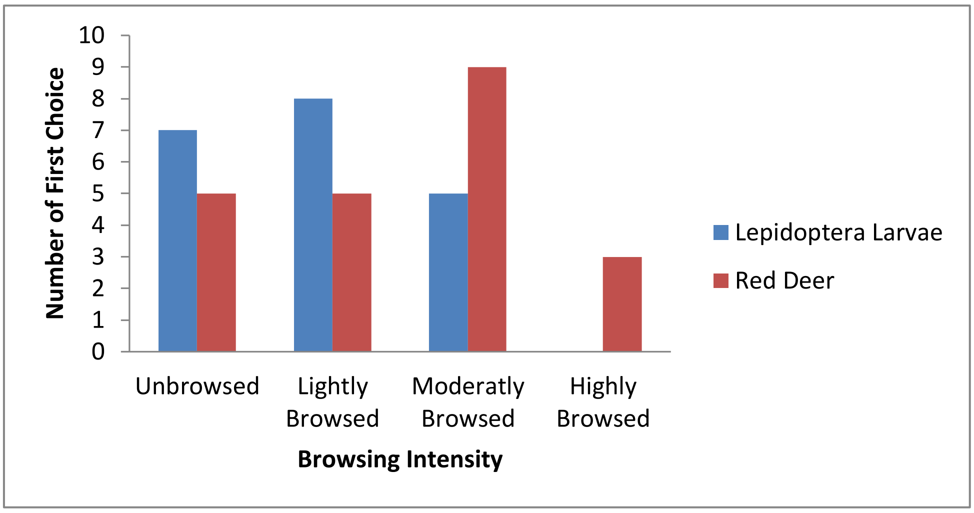

Figure 2: The first choice of Lepidoptera larvae and red deer. The larvae chose the lightly browsed leaves most frequently, while deer chose the moderately browsed bilberry most frequently. No larvae chose the highly browsed leaves as their first choice, while three deer did chose the highly browsed plants.

When first choice was analysed separately, larvae appear to be more selective than deer in food choice. Larvae made a conscious first choice of food with different browsing intensity (Monte Carlo approach, P- value = 0,015). Deer did not differentiate between the different browsing intensities (Monte Carlo approach, P- value = 0, 3625). When preference in first choice was compared between larvae and deer, no difference in preference was detected (Fisher's Exact Test, df= 2, p-value = 0.197, P > 0, 05). The size of the leaf did not influence larvae first choice (Multinomial Logistic Regression, P- value = 0.1081, P > 0, 05).

Both deer and larvae avoided the intensively browsed bilberry (Exact Binomial Test, P- value > 0,001). Only two stags took part in the first choice trial, and both stags chose the highly browsed bilberry as their first choice. Due to the low amount of males, no test could be executed to investigate any differences in sexes and first choice.

Discussion

Previous studies have reported that damage may induce defence in plants (Bryant 1981), making them less favourable for herbivores (Ayres et al. 1997; Haukioja and Niemelä 1977). Other studies have found that light (Bergqvist et al. 2003; Williams and Myers 1984) or even intensive browsing (Dahlgren et al. 2007) will increase the palatability for herbivores. My prediction, that deer is less selective in food choice compared to larvae, seems to be confirmed by my results. In this study, larvae preferred the lightly browsed bilberry, both in the amount of consumed leaf tissue and first choice. Deer chose the moderately browsed bilberry as first choice most frequently.

My results seem to support the existing evidence that presume ruminant herbivores to be less selective than larvae in choice of food. For larger herbivores there has been some evidence to support a “mild” avoidance strategy among roe deer (*Capreolus capreolus*) (Tixier et al. 1997), moose (*Alces alces*) (Stolter et al. 2009) and domestic lambs (*Ovis aries*) (Villalba et al. 2002), were the choice of food depends not only on defence substances present, but on nutrition value and the quantity available as well. It is likely that deer have similar food selection criteria. Evidence suggest that deer with a more advanced digestion systems would be less affected by defence substances in plants compared to non-ruminants herbivores (Meisingset 2008) and in turn insects. In addition, white tailed deer have been found to have proteins in their saliva that can bind and neutralize certain defence substances (Austin et al. 1989; Robbins et al. 1987). For larvae, defence substances have been reported to have strong negative effect on development and growth (Honěk 1993; Williams and Myers 1984). Seldal et al. (1994) found that the leaf beetle (*Galerucella lineola*) avoided grey alder (*Alnus incana*) that had been previously attacked. Moreover, the defence substances in grey alder affected retarded growth, delayed pupation, reduced egg production and the overall low survival of the leaf beetle (Seldal et al. 1994).

Larvae selected significantly more of the lightly browsed leaves in both leaf consumption and first choice, indicating that larvae found less browsed plants more palatable. These findings support my prediction; that previous heavy browsing affects bilberry palatability negatively. Similar to my results, Williams and Myers (1984) found that previously attacked red alder (*Alnus rubra*) by western tent caterpillar (*Malacasoma californicum*) improved food quality for fall webworms (*Hyphantria eunea*). In addition, larvae feeding on intensively attacked trees had a slower development and smaller size, while larvae feeding on trees with light damage grew faster, and achieved a greater pupal weight than those that fed on trees not previously attacked (Williams and Myers 1984). It’s been proposed that insects may find regrowing tissue more palatable than unbrowsed plants because of the high nutrition value in the developing tissue (Heichel and Turner 1983; Volenec et al. 1996; White 1978). This would indicate that light browsing may in some cases benefit certain insect species.

Both deer and larvae avoid the highly browsed plants. Other studies have come to a similar conclusion (Bryant 1981; Schultz and Baldwin 1982), indicating that high browsing intensity deteriorate food quality. This study indicates that artificially high browsing intensity may affect bilberry palatability even for ruminants with advanced digestive system. However, deer seemed to prefer the moderately browsed plants which were the most frequently observed first choice. This may indicate that normally high deer densities will not have an effect on ruminants food choice, because deer densities on Svanøy are thought to be representative for western Norway (J.T. Solheim; S.J. Hegland, personal communication, 2014).

The strength of this study was that I utilized plants previously browsed by deer over several decades in a natural ecosystem, and not simulated browsing. I also used natural sized leaves and plants in order not to unintentionally induce defence substances which may have affected food choice. I found that leaf size did not influence larvae first choice. However, the highly browsed leaves were never selected as larvae first choice. The highly browsed leaves were generally smaller in size compared visually to the other leaves, and it may have had an effect I was unable to detect. In my study only two stags participated, and both chose the highly browsed plants as their first choice. Other studies have found evidence for a difference in diet between sexes, were hinds generally had a higher quality diet compared to stags (Beier 1987). Due to my small sample size I chose to include the stags in my test. I did not investigate the soil richness and therefore cannot determine the relative productivity of the sites. Pedersen et al. (2011) found that voles (*Microtus oeconomus*) preferred bilberry from high productivity sites, compared to that of low productivity site, with the same amount of browsing intensity. This indicates that browsing alone does not explain the entire food choice. The soil richness is also thought to be an important factor for whether plants produce defence substances, or allocate recourses for growth (Herms and Mattson 1992; Pedersen et al. 2011).

Deer populations in both Europe and America have expanded during the last decades (Gill and System 1990), and concerns for the ecological consequences of intensive browsing have increased accordingly (Côté et al. 2004; Mysterud et al. 2010; Mysterud et al. 2002). Bilberry is a dominant species in the boreal forest systems and serves as a host plant for many vertebras and invertebrates. The flower is an important source of nectar (Jacquemart 1993), the plant itself is an important habitat for both vertebras (Hjeljord 2008) and invertebrates (Jacquemart 1993), and the berries is an important food source for many birds (Hjeljord 2008). The effects of browsing pressure on bilberry affect plant morphology and density (Pigott 1983; Waller and Alverson 1997), which in turn may affect the insect composition and density, because plant species richness and plant functional groups are often positively correlated with insect species richness (Haddad et al. 2001; Murdoch et al. 1972). This again may have management implications for many forest birds such as Capercaillie (*Tetrao urogallus*) and Black Grouse (*Tetrao tetrix*) as they depend upon bilberries and insects, especially Lepidoptera larvae, for food as young chicks (Atlegrim and Sjöberg 1995; Wegge and Kastdalen 2008). This way high densities of ungulates in forest system have the potential to create cascading effects by alter food quality for other herbivores by inducing defence substances in plants. Rooney and Waller (2003) theorize that if deer densities become very high it could limit the overall biological diversity.

Conclusion

Both Lepidoptera larvae and red deer avoided the intensively browsed bilberry. Deer appeared to prefer the moderate browsing intensity. I conclude that larger herbivores do not show a strong selection against previously browsed bilberry plants. Lepidoptera larvae prefer lightly browsed bilberry, supporting the hypothesis that because of insects simple digestive system, insects are more sensitive to plant defence substances. This would indicate that at naturally high browsing pressure, some insect species, including Lepidoptera larvae, may be negatively affected. More research is needed in order to determine how deer browsing might affect insects.

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