Thomas B. Berg

Catechin content and consumption ratio of the collared lemming

Abstract Chemical – plant defences as mechanisms affecting herbivore populations have been debated during the past decade. Several authors have questioned the hypothesis, but the present study shows that collared lemmings (*Dicrostonyx groenlandicus*) in northeast Greenland prefer food plants with a lower catechin content. *Dicrostonyx* species are known to have specialised on shrubs, especially *Dryas* spp. and *Salix* spp., rather than graminoids like other related microtines. Bioassays were conducted using food material from *Dryas* spp., *Salix arctica*, *Vaccinium uliginosum*, *Kobresia myosuroides* and *Poa glauca*. Enclosures with the first three species mentioned were further treated by clipping to simulate herbivory in order to induce the production of the plant defence compound catechin. Treatment increased the catechin content in *Dryas* spp., *S. arctica* (females only) and *V. uliginosum* significantly compared with the catechin concentration in untreated plants. These elevated catechin concentrations had a significantly negative effect on the consumption rate of *Dryas* spp. and female *S. arctica* by collared lemmings.

Keywords *Dicrostonyx groenlandicus* · Greenland · Phenol · Plant defence · Plant – lemming interaction

Introduction

The relation between food quality and food preference is highly complex. Palatability may differ among plant species (Batzli and Lesieutre 1991), whereas protein

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content and secondary plant components change during the growing season (Batzli 1983; Lindroth and Batzli 1986) and are also affected by herbivory (Lindroth and Batzli 1986; Gadd et al. 2001). Secondary plant components are known to affect the food choice of herbivorous insects (Agrawal 1998; Underwood 2000), birds (Selås 1997; Guglielmo et al. 1996) and mammals and to reduce their reproductive output (Jung and Batzli 1981; Batzli 1983; Moen et al. 1993; Seldal et al. 1993). However, high concentrations of secondary plant components can be tolerated if the food plants contain sufficient levels of protein and nutrition (Marquis and Batzli 1989). Conclusions on the effect of chemical plant defences on herbivores therefore often depend on the specific food plant concerned and the herbivore species investigated (see Plesner Jensen and Doncaster 1999). Carbon and nitrogen play different functional roles in the chemical defences of plants (McKey 1979; Bryant et al. 1983, 1993) and different plants may hence respond differently to specific shortages in soil nutrition. The response to herbivory also depends on factors such as timing, type and history of herbivory (Lundberg et al. 1994; Rosenthal and Kotanen 1994; Gadd et al. 2001).

As plant defence mechanisms reduce the digestibility of food plants, they have played a key role in the plant – herbivore hypothesis of cyclic microtine populations (Batzli 1983; Seldal et al. 1993; Plesner Jensen and Doncaster 1999). Plant defences have been hypothesised to increase in response to herbivory, reducing the quality of the food plant, and the fitness of the herbivore, and thereby initiating the crash or decline of their populations. This phenol-based hypothesis, however, has been questioned in several studies (Krebs 1964; Oksanen et al. 1987; Moen et al. 1993, Klemola et al. 2000) and has primarily been focused on the most preferred food plants while ignoring alternative, less-preferred food plants to which the herbivores switch after depletion of their preferred food resource. Plesner Jensen and Doncaster (1999) found that these less-preferred food plants often had the ability to produce toxic or lethal secondary plant components that may cause the population crash. In

contrast to the preferred food plants the marginal food plant species were heavily browsed only during peak herbivore densities. It appeared that secondary food plants induce the production of chemical defences highly efficiently, whereas the preferred primary food plants tend to invest in compensatory growth instead of chemical defence.

This paper focuses on food consumption rates by the high arctic collared lemming (*Dicrostonyx groenlandicus*) in northeast Greenland in relation to the catechin content (phenol-based precursor of proanthocyanidins) of its food plants. I hypothesise that herbivory induces the production of catechin and that catechin as a chemical plant defence negatively affects the amount of plant material eaten by lemmings. I test this hypothesis using simulated herbivory and bioassays measuring the consumption rates of five food plant species with different catechin concentrations.

Materials and methods

The collared lemming inhabits some of the harshest arctic environments and is specifically adapted to this kind of ecosystem. Along with the musk ox (*Ovibos moschatus*) and Arctic hare (*Lepus arcticus*) the collared lemming is the only resident mammalian herbivore in northeast Greenland. The collared lemming exhibits dramatic changes in population density in a 4- to 5-year cyclic period. As a key prey for a number of predators and through plant–lemming interactions, this microtine may be regarded as a key species in the simple High Arctic ecosystem where it can indirectly affect other trophic levels (Sutherland 1988; Sittler et al. 2000; Blomqvist et al. 2002). Lemming winter quarters are placed at sites with a dense and stable snow cover to protect them from winter storms and temperatures well below −20°C (Thomsen and Rasch 2000). Summer habitats are dry and free of snow early in the season and are mainly used for burrows in the soil for nests and retreat. Due to much higher numbers of predators during summer, lemmings exploit their home ranges intensively around the burrow entrances and may hence affect the local vegetation around burrows more heavily than they do around winter nests during winter. Having examined more than 3,000 winter nests and their surroundings I have only occasionally experienced local depletion of food plants in the field, mainly *Vaccinium uliginosum* stands, which in addition is not one of the main winter food plants for *D. groenlandicus* (Batzli 1983; T.B. Berg, in preparation). *V. uliginosum* is one of those less-preferred food plants that can produce toxic secondary components (Plesner Jensen and Duncaster 1999).

Bioassays

Field experiments were carried out at Zackenberg, northeast Greenland (74°28'N, 28°34'W) in a year (2000) with low lemming density. Three subadult collared lemmings (weighing 25, 25, and 30 g) were caught in the field using baited Ugglan live traps on 5 and 6 July and were kept individually in cages until release on 31 August. The cages were 0.6-m² open-top wooden boxes covered with aviary net and placed outside in the open, protected against northerly winds. A smaller closed wooden nest box was offered as shelter inside the cage. Captive lemmings were fed daily ad libitum with fresh leaves from *Salix arctica* (females and males treated separately in all analyses)*, Dryas* spp.*, Poa glauca*, *V. uliginosum* and *Kobresia myosuroides*.

Consumption rates of plant material based on fresh weight are highly correlated with corresponding rates based on dry mass (Hjáltén et al. 1996). In this study I followed the procedure developed by Hjáltén et al. (1996) and used only fresh weight for all analyses. Differences in consumption rates with respect to plant species and catechin concentration were investigated through two types of bioassays in the open-top wooden boxes. All food servings were prepared separately for each plant species and catechin level (see below) and divided into four portions weighed to the nearest 0.01 g. One portion was offered to each of the three lemmings and the fourth portion was placed in a similar open-top wooden box without a lemming to serve as a weight control. The bioassays were kept under regular observation and were terminated before any of the food dishes were emptied. The duration of the bioassays varied between 2.5 and 8.5 h (mean duration 5.5 h). At the end of each bioassay nest boxes were checked for any stored food, and all remaining food plant material left in the petri dish was weighed in order to measure the amount eaten. The controls were used to estimate the food plant specific rates of weight loss due to the varying duration of the bioassays and the weather-dependent desiccation rates during the experiments. Weight control samples from both bioassay 1 and 2 were then dried at room temperature in paper bags to allow further analysis after the field season.

Bioassay 1 used material of leaves arbitrarily collected in a single area of 1,000 m² at a south-facing slope with dwarf-shrub heath vegetation [later used as untreated control for the treated plants (simulated herbivory) in bioassay 2]. The five different plant species were offered immediately after harvest on 8, 10, 12, 21 and 30 July and on 1 and 4 August, giving the lemmings the opportunity to select among all five species. Each plant species was served in a separate glass petri dish at equal distances from the nest box.

In bioassay 2, lemmings were given the opportunity to select among four levels of catechin concentrations within a single plant species (*Dryas* spp., *S. arcitca*, *V. uliginosum*). These levels were induced by controlled simulated herbivory on 160 enclosed plants (40 of each species, enclosed area: 755 cm²) in a dry *Dryas* heath. All three food plant species were treated with four intensities of simulated herbivory (four categories) with 10 replicates each (Table 1). After the final clipping, all remaining leaves within the 160 enclosures were sampled and pooled according to species and the four categories of simulated herbivory in order to obtain enough food material for the bioassay. Due to the change of leaf colour, *S. arctica* was only clipped three times with 8 August as the last date. Each bioassay (in bioassay 2) contained only one plant species at a time to test exclusively whether the lemming discriminated between the expected four levels of induced catechin concentrations from the four categories of simulated herbivory. These four levels of catechin concentrations were kept separate in glass petri dishes placed at equal distances from the nest box in the open-top box. The dishes were relocated every hour to eliminate as far as possible the possibility that lemmings would learn to use indirect position cues to select their food.

After the field season the dried control plant material from both bioassays was ground with a grinding mill and pestle and mortar. The content of catechin was analysed colorimetrically using the vanillin:HCl test with catechin as the standard (Julkunen-Tiitto 1985).

Statistical analysis

The amounts of the various plant species eaten are expressed as consumption rates (g/h) (adjusted for desiccation losses). Food preferences of the six plant species were analysed by ANOVA after arcsin transformation (Sokal and Rohlf 1995) of the consumed percentage of total plant mass making the data approximately normally distributed. Preferences between specific food plants were tested by Tukey test following the ANOVA (Sokal and Rohlf 1995). A Kruskal-Wallis test (Sokal and Rohlf 1995) was used to test for species-specific differences in catechin concentration [adjusted for day of year (DOY)] between treatments (pooled data from categories 1–4) and untreated (controls from bioassay 1). General linear models (GLM, Lindsey 1999) were used to analyse

Table 1 Simulated grazing was made by clipping entire leaves from the enclosed plants up to 4 times during the summer using a pair of tweezers. Each category consisted of ten replicates. From the *Salix arctica* enclosures ten fully developed leaves were removed from the distal part of ten randomly chosen branches within each enclosure (one leaf per branch). From the *Dryas* spp. and *Vaccinium uliginosum* enclosures 100 green leaves were randomly sampled within a permanently marked 10×10-cm quadrat inside the enclosure. Each cell shows the number of leaves removed from the relative category number stated in the second column. *Dryas* spp. and *V. uliginosum* share the last four rows with categories 1–4 and have 100 leaves clipped each

Species	Category	10 July clipping	26 July clipping	8 August clipping	15 August clipping
S. arctica	1	10	10	10	None
	2			10	None
	3		10	10	None
Dryas spp. and *V. uliginosum*	1	100	100	100	100
	2			100	100
	3		100	100	100
	4				100

the relations between consumption, intensity of simulated herbivory (Category), DOY, plant species (Plant), treatment (simulated herbivory or control), catechin concentration (Catechin), and starting weight of served food (Start weight). Tukey-Kramer's test was used for comparing a set of regression lines (Sokal and Rohlf 1995). In order to focus on the effect of catechin concentration on the consumption rate by lemmings only plant species that were treated with simulated herbivory were used (*Dryas* spp., female and male *S. arctica*, and *V. uliginosum*).

A total of four GLM models were applied:

Model 1. Catechin concentration =

$\beta_0 + \beta_1 Category + \beta_2 DOY + Treatment + \beta_3 Category \times DOY + Category \times Plant + DOY \times Plant + Category \times DOY \times Plant$,

analysing the effect of the four levels of simulated herbivory on catechin concentration.

Model 2. Catechin concentration =

$\beta_0 + \beta_4 DOY + Plant + \beta_5 Treatment + DOY \times Plant + \beta_6 DOY \times Treatment + Plant \times Treatment + DOY \times Plant \times Treatment$,

analysing the overall effect of simulated herbivory versus control.

Model 3. Ln(consumption rate) =

$\beta_0 + \beta_7 DOY + Plant + \beta_8 Catechin + \beta_9 Start\ weight + DOY \times Plant + DOY \times Catechin + Plant \times Catechin + DOY \times Plant \times Catechin$,

analysing the overall effect of catechin concentration on consumption rate.

Model 4. Species-specific ln(consumption rate) =

$\beta_0 + \beta_{10} DOY + \beta_{11} Catechin + \beta_{12} Start\ weight + \beta_{13} DOY \times Catechin$,
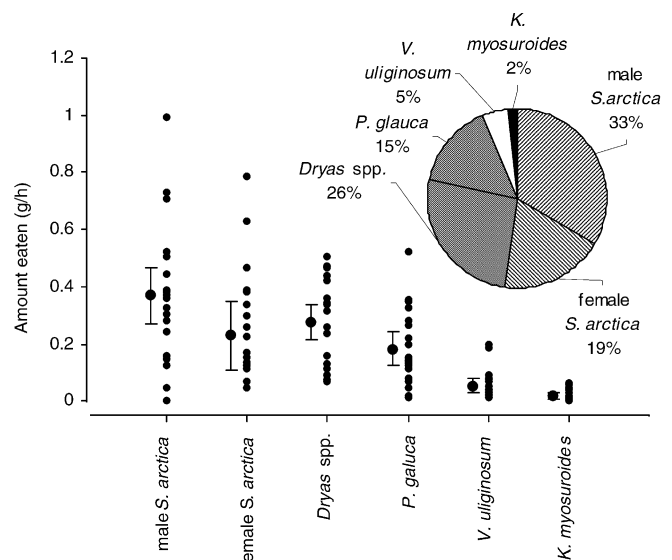
analysing the species-specific effect of catechin concentration on each of the three treated food plant species.

All statistical analyses were performed as forward stepwise interactive regression with α to enter <0.15 and using the software package Systat 8.0 for Windows (SYSTAT 1998).

Results

The body weight of all three animals used for the bioassays increased from 25, 25, and 30 g to 34, 41, and 39 g, respectively, during 57 days of captivity (5 July–31 August). During the bioassays no difference in consumption ratios were found between the three animals adjusted for DOY, plant species, and starting weight (GLM, $F_{animal(2,126)}=0.57$, $P=0.57$). Figure 1 shows the results from the seven runs of bioassay 1. Arcsin-transformed data showed that *V. uliginosum* and *K. myosuroides* had a significantly lower rate of consumption than all other

Fig. 1 Consumption rates (g/h) of the food plant species by three collared emmings (*Dicrostonyx groenlandicus*) during seven "replicates" (seven harvests) of bioassay 1. Both the original data and means ± SE are given. The *pie chart* in the upper right corner of the figure shows the mean proportional consumption ratio for the three lemmings with seven replicates of bioassay 1 each, $n=21$. The scale of the figure does not allow differentiation between all 21 *dots* within each plant species

species in the analysis and. *P. glauca* and female *S. arctica* had significant lower consumption rates than male *S. arctica* (Tukey test$_{(6,120)}$, $P<0.05$). Nevertheless, especially *K. myosuroides* is often heavily grassed close to the entrances of lemming summer burrows. The difference in consumption rate between the two sexes of *S. arctica* was positively related to the generally higher catechin concentration (mg/g) found in female leaves over the summer (39.28±5.01 SE) compared to males (25.87±2.96 SE). This difference in catechin concentration was, however, not significant (*t*-test, two-tailed, $P=0.231$ N: seven males, seven females). Catechin concentrations in the other food plants were *P. glauca*: 1.67±0.18 SE, *K. myosuroides*: 3.91±0.40 SE, *Dryas*: 15.47±1.75 SE, and *V. uliginosum*: 123.63±20.16 SE.

Fig. 2 Change in catechin concentration over the field season of four lemming food plant species. Simulated herbivory treatments (*filled dots*) and controls (*open dots*). Note the different scaling of the *y-axis*. The slopes of two *regression lines* are significantly different from zero within: *Dryas* spp. treatment (R^2=0.147, P=0.006, n=50) and female *Salix arctica* treatment (R^2=0.159, P=0.029, n=30). All comparisons of treatment versus control regression lines except the two in male *S. arctica* have significantly different slopes (P= 0.05, Tukey-Kramer test: unplanned comparisons among a set of regression coefficients, Sokal and Rohlf 1995)
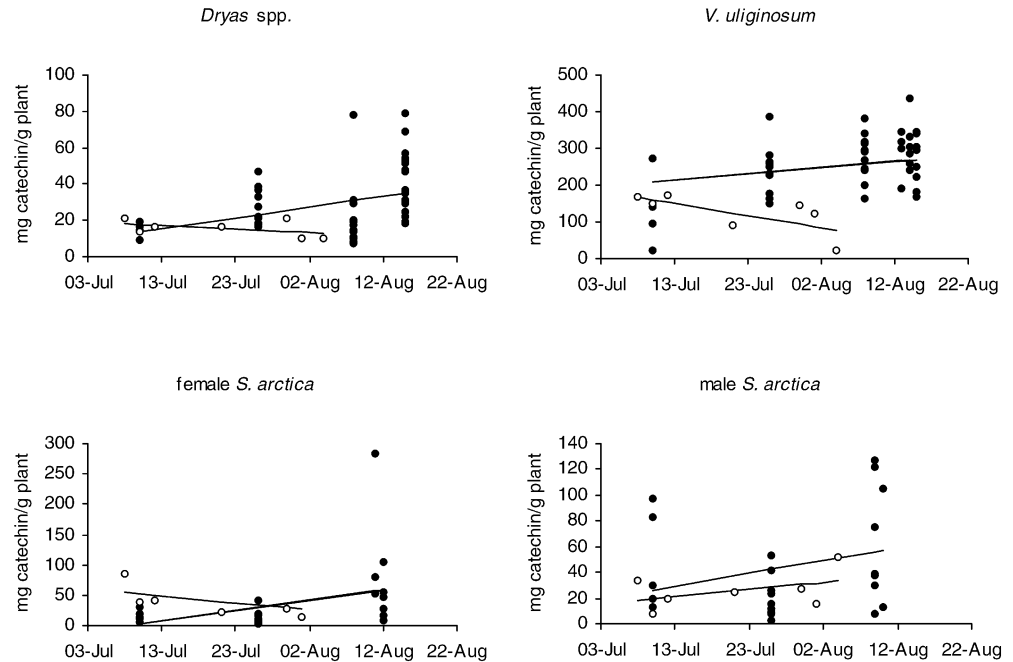
Table 2 Result of the catechin concentration as a function of day of year (*DOY*), plant species (*Plant*), treatment, and their interactions (GLM model 2, DOY was forced into the model at the beginning) as well as the result of the overall log_e-transformed consumption rates as a function of DOY, Plant, catechin concentration (*Catechin*), starting weight of the served plant species (*Start weight*) and their interaction (GLM model 3, DOY and Start weight were forced into the model at the beginning). A stepwise forward interactive procedure was used. Only those independent variables with α to enter <0.15 were included. Species included: *Dryas* spp., female and male *Salix arctica*, and *Vaccinium uliginosum*.

Independent variables	β_i	Sum of squares	df	% explained	F-ratio	P
GLM model 2: Catechin conc. = β_4DOY+Plant+β_5Treatment+β_6DOY×Treatment ; n=42; R^2=0.819						
DOY	−1.025	3,233.683	1	1.7	4.896	0.034
Plant	N/A	77,964.990	3	72.2	39.348	0.000
Treatment	−1210.034	3,199.043	1	7.0	4.844	0.034
DOY×Treatment	5.611	3,424.907	1	2.7	5.186	0.029
Error		23,116.548	35			
GLM model 3, Catechin conc. = β_7DOY+Plant+β_8Catechin+β_9Start weight+DOY×Plant+Plant×Catechin+DOY×Plant×Catechin; n=153; R^2=0.559						
DOY	−0.018	1.034	1	9.0	1.194	0.276
Plant	N/A	7.916	3	3.2	3.047	0.031
Catechin	−0.018	6.707	1	0.9	7.745	0.006
Start weight	0.054	0.965	1	24.7	1.114	0.293
DOY×Plant	N/A	7.815	3	7.9	3.008	0.032
Plant×Catechin	N/A	16.452	3	4.2	6.333	<0.001
DOY×Plant×Catechin	N/A	16.239	3	6.0	6.251	0.001
Error		118.638	137			

The simulated herbivory within the 160 enclosures ranged between 20% and 60% of the total number of green leaves depending on category. GLM model 1 showed no overall significant effect of the four categories of simulated herbivory on catechin concentration based on data from the whole season (P=0.74). Neither did the species-specific analyses of catechin concentrations among the four categories at the last harvest show any significant difference (P>0.378). All categories of simulated herbivory were therefore pooled within each species and used as "treated material" in further analyses. All four treated plants increased their catechin content over the season while the control showed a tendency for catechin concentration to decrease during the same period (Fig. 2). The significantly different slopes of treatment versus control in *Dryas* spp., female *S. arctica*, and *V. uliginosum* shown in Fig. 2 likely reflect the effect of simulated herbivory on the plants.

GLM model 2 showed that both DOY, species, treatment, and the interaction of treatment and DOY had a significant effect on catechin concentration (Table 2). The effects of "treatment" versus control at the food plant species level were further tested by Kruskal-Wallis tests. Significant differences between treatment
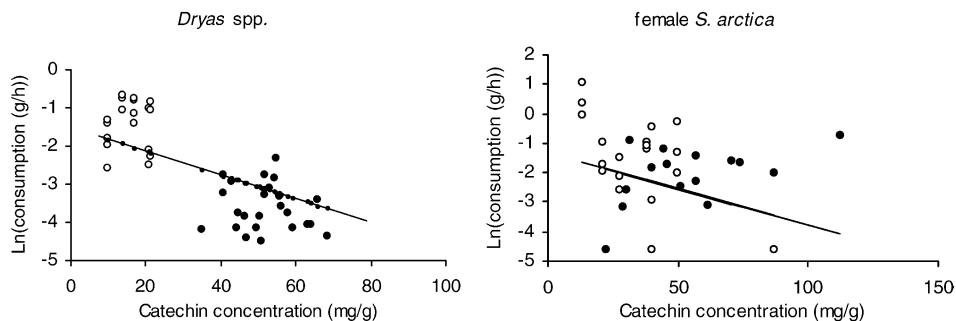
Fig. 3 Relation between log$_e$-transformed consumption rate and catechin concentration [adjusted for day of year (DOY) and starting weight]. *Open circles* represent control samples and *filled circles* represent pooled samples from simulated herbivory treatment. *Regression lines* are derived from the species-specific models in GLM model 4 including the independent variables: DOY, catechin concentration (Catechin) and starting weight of the served food plant (Start weight), coefficients in *bold* are significant (P<0.05): *Dryas* spp.: ln(consumption rate) = 6.157–0.036DOY–0.031Catechin+0.033 Start weight, R^2=0.774, F=46.870, P<0.001, n=45 female *S. arctica*: ln(consumption rate) = 17.346–0.094DOY–0.444 Catechin+0.167 Start weight+0.002DOY×Catechin, R^2=0.413, F=5.444, P=0.002, n=36

Table 3 Kruskal-Wallis test of the species-specific effect of treatment versus control expressed as catechin concentration (mg/g plant material). Data cover all samples over the season

Species	Control mean ± SD, n	Treatment mean ± SD, n	P-value
Dryas spp.	15.474±4.641, 7	29.266±17.938, 50	0.027
Female *S. arctica*	39.278±24.213, 7	39.416±53.747, 30	0.278
Male *S. arctica*	25.874±14.318, 7	46.888±42.300, 30	0.438
V. uliginosum	123.631±53.328, 7	257.745±78.991, 48	<0.001

and control were found in *Dryas* spp. (P=0.027) and *V. uliginosum* (P=0.006) (Table 3).

The results of GLM model 3 showed an overall significant negative effect of the catechin concentration on the consumption rate adjusted for DOY and start weight. (Table 2). As species and catechin concentration both had significant effects, the analysis continued with the species-specific GLM model 4 showing significant negatively effects of catechin concentration on the log$_e$-transformed consumption rate (g/h) (adjusted for DOY, start weight and catechin concentration×DOY) in *Dryas* spp. and female *S. arctica*, (Fig. 3) while male *S. arctica* and *V. uliginosum* did not show such an effect.

Discussion

In general, using only three animals for repeated feeding experiments creates a statistical problem with pseudoreplication because the animal-related errors are related to these three animals only and not to the sum of repeated experiments. The effect of animal in the GLM analysis had no effect on the consumption rates, however (P=0.57). To have the opportunity to run the cantina experiments several times I accepted the use of pseudoreplicates as trapping other lemmings in a low-density situation was difficult. This should be kept in mind when interpreting the results.

The summer food consumption rates derived from bioassay 1 corresponded well with results from faecal analysis from other parts of north Greenland where winter pellets from collared lemmings contained 63% *Salix* spp. and 24% forbes (including *Dryas* spp.) (Klein and Bay 1991). At Point Barrow (Alaska) Batzli and Pitelka (1983) made stomach analyses of collared lemmings in dry ridge habitats in June, and found 45% *Salix* spp., 19% *Potentilla*, 8% *Draba* but only 4% *Dryas* spp.. Mid-September food preference on Truelove Lowland was found to include 42.9% *Dryas integrifolia*, 36.9% *Saxifragas oppositifolia*, and 12.3% *S. arctica* (Fuller et al. 1977). Despite the observed locally heavy browsing of *K. myosuroides* around summer burrows at Zackenberg this species turned out to be the least-preferred food plant among the five different plant species offered during bioassay 1. This may indicate that the collared lemmings living on the open tundra at Zackenberg are forced to utilise all potential food items without expressing accurate preferences due to the high risk of predation in the area (Schmidt et al. 2002; Berg 2002). A study by Klemola et al. (2000) showed that field voles (*Microtus agrestis*) were unaffected by previous heavy grassing on grasslands. Field voles are graminivores and graminoids depend more on regrowth than investment in chemical plant defences. In the present study catechin levels in *K. myosuroides* (sedge) and *P. glauca* (grass) were orders of magnitude lower than those found in *Dryas* spp. *S. arctica* and *V. uliginosum* (shrubs).

Consumption rates of male *S. arctica* were significantly higher than of female *S. arctica*. Although the present data did not show significant differences in

catechin concentration between males and females, the difference in consumption rate might relate to the lower content in males than females, a difference that is probably related to sex-specific differences in investment in reproduction. Investment by males terminates early in the season, while the investment by females last until the end of seed development, so that prolonged protection is required. Predavec and Danell (2001) found no feeding preference during winter towards male *Salix lantana* based on scarring marks in the bark. They mentioned though that male-biased herbivory on *Salix* might be less pronounced during peak population densities than in low-density years. In discussing feeding preferences between male and female *Salix* species, seasonal differences should be considered as different parts of the plant are consumed and chemical plant defences are distributed unevenly within plants (McKey 1979; Bryant 1981). The amount of food plant material used in the bioassays did not allow such differentiation of the offered food plants into young and old leaves and twigs.

Although no differences in catechin concentration were detectable among the various levels of simulated herbivory, the catechin concentration increased over the season in contrast to the untreated controls of leaves arbitrarily collected in a single area of 1,000 m^2 at a south-facing slope with dwarf-shrub heath vegetation. As in the untreated control, a similar seasonal decrease in concentration of various secondary compounds was found in *Betula nana* at Abisko, Swedish Lapland (Graglia et al. 2001), but Riipi et al. (2002) found no change in the catechin concentration over the summer in mountain birch (*Betula pubescens* subsp.). As plants do have the ability to communicate the detection of herbivory to neighbouring relatives as well as other plant species (Bruin et. al. 1995; Penuelas et al. 1995; Shulaev et al. 1997) this may explain the failure to detect any differences in catechin concentration between categories of simulated herbivory due to the relative short distances between the individuals in the sampling enclosures.

In an evolutionary context one would expect that secondary plant components to be detectable by herbivores in order to save the plant from being eaten. Microtines fed on low-quality food will increase their intake in order to meet their nutritional requirements (Batzli and Cole 1979). If a lemming consumes food containing high levels of thrypsin inhibitors it will suffer from malnutrition due to the unavailability of proteins bound to these inhibitors and may die independent of the amount consumed (Jung and Batzli 1981; Seldal et al. 1993). By testing the species-specific consumption rate against catechin content (adjusted for DOY), lemmings showed the ability to select food material with less catechin in *Dryas* spp. and female *S. arctica* (Fig. 2).

Turchin and Hanski (2001) have argued that herbivore–plant and predator–prey data sets from different geographical regions may fit different explanatory hypotheses. Furthermore, different species of rodents may respond differently to chemical plant defences (Jung and Batzli 1981; Turchin et al. 2000).

Different species of microtines may play different roles within the same trophic level. Comparing vole and lemming fluctuations in Fennoscandia, Turchin et al. (2000) showed that the characteristic shapes of cyclic population curves of voles and lemmings were different. Voles exhibited rounded peaks with population maxima extending over 2 years, which is typical for a self-limiting and predator-driven cyclic interaction. In contrast, the shape of the specialist predator peak is sharply pointed because the predator populations quickly decrease, as their prey becomes scarce (resource driven cycles). In habitats with low production, such as in barren or arctic-alpine areas, the primary production is critically low, making the mammalian predator community dramatically resource-limited due to generally low prey densities. The diversity of predator species is correspondingly low. This drives the ecosystem towards a one-link trophic dynamic, and hence the lemming fluctuation tends to be resource limited like, for example, the stoat (Oksanen and Oksanen 2000). Lemming populations in such habitats in both Fennoscandia (Turchin et al. 2000) and northeast Greenland (Sittler 1995; Berg 2001) exhibit sharply pointed peaks with positive skewness values of log-transformed densities similar to specialist predators, which indicates that these lemming populations are not only driven by predators. Especially during summer peak densities, their resources may be overexploited or, being too low in quality due to plant defences, make the lemming more vulnerable to predators.

During summer, lemmings spend between 57% and 88% of their time in the burrows and while outside they use 14–55% of the time watching and 36–76% feeding. All these activities are concentrated within 3 m from the burrow entrance (Kyhn and Berg, in preparation). A radiotelemetry study by Boonstra et al. (1996) indicated that lemmings might even spend up to 95% of their time in their burrows. Not surprisingly this leads to heavy browsing and high stress on the plants close to the burrow entrances. Lemmings may therefore have few opportunities to choose among individual food plants with low concentrations of catechin. Hence, nutritionally stressed animals may be forced to spend more time foraging in the open, which increases their risk of being killed by predators. If lemmings are forced to ignore chemical plant defences, especially those inhibiting the protein uptake (Seldal et al. 1993), the protein content in their faeces may be expected to change during the season and among years in response to changes in population densities during the lemming cycle (T.B. Berg, in preparation). At Zackenberg, the occupied summer habitats tend to have a bigger overlap from year to year than winter habitats (Berg et al., in preparation) and the grazing pressure per area may differ across seasons and years accordingly. This may lead to a generally higher level of chemical plant defence in summer food plants than in winter food plants. No lemming populations in Greenland have been reported as increasing in number over the summer, whereas stable densities or population declines seem to be the rule (Sittler 2000; Berg 2002). The long winters

with relatively easy access to food resources and fewer predators may probably be the key factors that enable the lemming populations to reach their well-known peak densities every f4–5 years, but comparable data on the amount of available food plant biomass during summer and winter are needed.

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