*Ann. Zool. Fennici* 50: 189–199 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 August 2013

# Vole damage to woody plants reflects cumulative rather than peak herbivory pressure

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*Received 13 Dec. 2012, final version received 11 Mar. 2013, accepted 18 Feb. 2013*

Gilbert, S., Norrdahl, K., Martel, J. & Klemola, T. 2013: Vole damage to woody plants reflects cumulative rather than peak herbivory pressure. — *Ann. Zool. Fennici* 50: 189–199.

Vole grazing may be a step-function, with a critical threshold density, at which voles expand their preferred diet to lower quality forage (threshold herbivory hypothesis). Accordingly, we predicted that the establishment of unpalatable woody plants would be more strongly associated with peak herbivore abundances than with cumulative herbivory at lower numbers. We also investigated whether damage level is better explained by actual vole numbers or by numbers adjusted to the carrying capacity of the herbaceous vegetation. Our results did not support the threshold-density hypothesis. Cumulative herbivory explained the probability of sapling damage better than peak herbivory; sapling survival and growth were equally well explained by mean- and peak-vole abundances. Even at low abundances, herbivory was extended to all woody species; the damage level, however, varied according to the palatability of the woody species. Actual herbivore numbers explained sapling damage better than did abundance adjusted to carrying capacity.

## Introduction

Most aquatic and terrestrial ecosystems are shaped by the complex interactions of trophic relationships, including both top-down and bottom-up forces (Gruner *et al*. 2008, Garibaldi *et al*. 2010, Estes *et al*. 2011). The mechanisms that regulate or limit herbivore numbers may affect the strength of top-down effects on plants (Oksanen & Oksanen 2000, Schmitz 2008). The characteristics of predator–prey dynamics may likewise influence the outcome of plant–herbivore interactions. In a stable systems where herbivore numbers are pressed by predators towards low or medium equilibrium points (Hanski *et al*. 1991), the impact for instance of vole grazing on grassland vegetation may be trivial (Crawley 1983). In contrast, at high densities herbivore populations can have a strong impact upon plants (e.g. Elton 1942, Batzli & Pitelka 1970, Hambäck *et al*. 2004, Howe *et al*. 2006, Huitu *et al*. 2009, Estes *et al*. 2011). Meadow voles (*Microtus pennsylvanicus*) can potentially retard old-field succession by hampering the growth and survival of woody plants (Gill & Marks 1991, Ostfeld & Canham 1993). It has also been suggested that the impact of cyclically oscillating herbivore populations on plants may be more pronounced than that of more stable herbivore numbers, as oscillating populations periodically reach high densities (Abrams 1999).

Mammalian herbivores generally select plants rich in nutritional components and poor in fibre and secondary metabolites, such as tannins (e.g. Hjälten & Palo 1992, Bozinovic 1997). Bozinovic (1997) showed that when small rodents are allowed to choose food that is low both in fibre and tannins, they strongly prefer such food. The fate of a fibre- and tannin-rich plant, such as a woody plant, may therefore depend more on the availability of high-quality food plants than on the edibility of the poor-quality plant itself. With increasing herbivore densities, the rising herbivory pressure on high-quality food plants depletes preferred food sources and forces consumers to expand their diet selection. This dietary expansion can take place either gradually or as a step-function. Norrdahl *et al*. (2002) suggested that the top-down effects of voles may be a step-function with a critical threshold density, whereby voles expand their diet from high quality food (preferred grasses and forbs) to poorer quality ones, such as tree seedlings and saplings. Accordingly, vole herbivory should impose serious damage on low-quality forage, such as most woody plants, only above the critical threshold density (Norrdahl *et al*. 2002). In predator-driven cyclic vole populations, where herbivore densities surpass the critical threshold more or less regularly but only for a short period, most damage to the saplings of woody plants should occur at these short vole peaks. In cyclic populations, the height of density peaks varies more than their duration (e.g. Norrdahl 1995), suggesting that the height of the density peak correlates with the extent of herbivory pressure above the assumed threshold line. Hence, the damage to woody plants should be more strongly associated with peak abundances than with the cumulative impacts of herbivory throughout vole population oscillation (as indicated by mean abundance).

Earlier studies have shown that woody plant palatability to mammals, including voles, varies greatly among species. Conifers are generally less preferred than deciduous species, although some studies have shown an opposite pattern (Vehviläinen & Koricheva 2006). There is, however, also variation among deciduous species: for instance *Alnus* is poor forage for voles, probably due to its secondary metabolites (Hjältén & Palo 1992), while *Populus* is relatively palatable to hares and voles (Hjältén *et al*. 2004). Although species in the Salicaceae family are generally accepted by herbivores (Gill 1992a, 1992b), Hjältén *et al*. (2004) found that they differ considerably in their palatability to herbivores. For instance *Salix myrsinifolia-phylicifolia* was not much utilized by hares and voles, probably because of its high concentration of phenolic glucosides (Tahvanainen *et al*. 1985, Hjältén *et al*. 2004). If the expansion of the herbivore diet from the most preferred herbaceous food to lower-quality plants is gradual, relatively palatable woody plants (e.g. *Populus*) should experience considerable damage at lower herbivore densities than the less palatable ones (e.g. *Alnus*).

We tested the prediction, based on the hypothesis of Norrdahl *et al*. (2002), that the top-down impact of vole herbivory on sapling survival would be more strongly associated with vole peaks than with the cumulative impact of herbivory at all abundances (as indicated by mean abundance). Based on the rationale presented above, we used the height of the vole peak (maximum abundance) as an index of herbivory pressure above the assumed threshold density. We also determined whether the expansion of vole herbivory from preferred herbaceous plants to woody plants is step-wise or occurs gradually as vole densities increase. Finally, we determined whether the level of herbivory damage on woody saplings is better explained by the actual abundance of voles or their abundance adjusted to carrying capacity of the herbaceous vegetation.

## Material and methods

### Study areas and experimental design

The study was carried out in two areas, Aura (60°N, 22°E) and Jokioinen (60°N, 23°E), in southwestern Finland, with three replicates (experimental fields) in each study area. The experimental fields were established in spring 2001 and data were collected from 2001 to 2003. The fields were located along small watercourses, crossing a slightly undulating but mostly flat agricultural landscape. The surrounding fields were drained with subsurface drainage systems and were under intensive cultivation with crop rotation between grass (silage) and arable crops (mainly cereal/oil rape).

Each of the six experimental fields consisted of a control (open) and three enclosed areas of 450 m$^2$ each. The experimental fields were treated as replicates, although there were some differences in cultivation history. The main differences between the experimental fields were that the three fields in Jokioinen were already covered by herbaceous vegetation in June 2001, whereas the three fields in Aura were established prior to the beginning of the experiment on the edges of organic rye fields by sowing a commercial seed mixture. The mixture consisted of *Phleum pratense* (40%), *Festuca pratensis* (35%), *Lolium multiflorum* (15%), and *Poa pratensis* (10%). The experiment was begun before a sward had developed at the Aura sites. Since peak densities of herbivorous voles depend on the quality and/or amount of food (Cole & Batzli 1979), and a peak in field vole populations is associated with a peak in biomass of the field-layer vegetation (Teivainen *et al*. 1986), we assumed that the experimental fields in Aura, with their sparser vegetation, would have a lower carrying capacity, and therefore lower potential peak densities than the experimental fields in Jokioinen. The difference between the study areas (Jokioinen and Aura) offered an opportunity to compare whether the level of herbivore damage was more closely related to the actual abundance of voles or to the abundance adjusted to the quantity of vegetation (assumed to indicate carrying capacity). On the other hand, the difference between the study areas led to difficulties in managing the vole numbers desired (*see* below for details). Within the study areas the experimental fields were located 500 to 5000 m apart, and were separated from cultivation by a grassy strip approximately one meter wide.

Enclosures were constructed of hardware cloth, with a mesh size 12.7 mm; they extended 60 cm below ground and 2 m above ground. Each area (30 × 15 m) was divided into two plots of 7 × 9 m each, separated and surrounded by a four-meter-wide mown strip. Saplings were planted in the plots in such a way that within each enclosure/control area one plot consisted of a monoculture of black alder (*Alnus glutinosa*), the other of a mixture of six species: black alder, Saskatoon serviceberry (*Amelanchier alnifolia*), downy birch (*Betula pubescens*), tea-leaved willow (*Salix phylicifolia*), *Populus tremula* (aspen) and *P. tremula* × *P. tremuloides* (hereafter referred to collectively as *Populus* spp.), and dark-leaved willow (*Salix myrsinifolia*). The phenotype of *S. myrsinifolia* indicated introgression by some other *Salix* species, possibly *S. phylicifolia*. Although these willows may have been hybrids rather than pure *S. myrsinifolia*, we refer to them as *S. myrsinifolia*. The *A. glutinosa* monoculture was established for the purpose of another experiment (Gilbert *et al*. 2013).

## Sapling introduction and monitoring

We planted saplings that were one to two years old (in the case of *Amelanchier* three years old) rather than smaller ones so as to ensure a safe start to our experiment, and to mimic the common practice whereby landowners introduce commercially available saplings at comparable sites, to prevent erosion, leaching and caving-in (Ministry of Agriculture and Forestry in Finland 2007). These woody-plant species were considered to be appropriate for this study, as they were expected to grow and become established in the nutrient-rich riparian field margins of agricultural lands.

The saplings were planted in spring 2001, immediately after the snow had melted; a total of 60 *Alnus glutinosa* saplings, or correspondingly 10 of each of the other species, were introduced in each plot. The spatial arrangement of the species in the plots was randomized. Individual saplings were spaced approximately 1 m apart. The first monitoring of the saplings was carried out shortly after their introduction, and was repeated at the end and at the beginning of the growing seasons, i.e. in September and June of 2001, 2002 and 2003. We recorded sapling growth (Table 1) and possible damage caused by voles gnawing on the bark. Sapling height was measured from the base at ground level (visible above-ground) to the highest living bud. Any sign of vole browsing, including minor damage, debarking and clipping, was always recorded binomially (i.e. damage or no damage; hereafter referred to as vole damage) as was the condition of the sapling or shoot, i.e. alive or dead. Small saplings can recover from vole clipping (Vandenberghe *et al*. 2008), and some saplings recorded as 'dead' actually produced new shoots during subsequent monitoring. In the statistical analyses, these saplings were treated as alive until the whole plant had died (did not produce new shoots).

## Vole introductions and live-trapping

*Microtus* voles were used in the study as a herbivore species. This is the main vertebrate herbivore species of boreal grasslands (Crawley 1983, Norrdahl 1995), with high-amplitude population cycles of three to five years (Norrdahl 1995, Klemola *et al*. 2000). The voles used in the study were predominantly field voles (*Microtus agrestis*). We also noted sibling voles (*M. levis*) in three areas. Both *Microtus* species are herbivorous and use similar although not identical food resources (Myllymäki 1977). As we were interested in general patterns rather than species-specific details, the two ecologically quite similar species were combined in the analyses.

The vole density treatment was started in November 2001, with four levels. In each of the six experimental fields (replicates), the open area was designated as a control area, representing the natural vole density at the study site. There was substantial variation in the natural vole density between the study sites. One pair of voles was introduced into one of the enclosures ('stable density' treatment level) and two pairs into another ('variable density' treatment level). One enclosure ('vole exclosure') was left empty and access by voles was made impossible by fences. Apparently some of the 'vole exclosures' were not totally vole-proof throughout the experiment, since within them we found some saplings that were damaged by voles, even though not a single vole was caught during the trapping periods. This resulted in some damage at 'zero' vole abundance. Shortly after introduction, initial vole numbers were estimated by live-trapping. Subsequently, the numbers were monitored four times in 2002, at two-month intervals (spring, early summer, late summer, late autumn), and once at the end of 2003. The vole numbers resulting from these live-trappings can only be viewed as minimum numbers of live voles.

**Table 1.** Initial mean heights (± SE) of six woody-plant species at the beginning of the experiment, measured shortly after planting (June 2001).

| Species | Mean height ± SE (cm) |
|---|---|
| *Alnus glutinosa* | 29.6 ± 0.4 |
| *Amelanchier alnifolia* | 26.8 ± 0.3 |
| *Betula pubescens* | 51.9 ± 0.5 |
| *Populus* spp. | 54.3 ± 1.0 |
| *Salix myrsinifolia* | 91.2 ± 0.8 |
| *S. phylicifolia* | 37.9 ± 0.5 |

In each enclosure, multiple-capture Ugglan live traps (Grahnab, Sweden) were placed in grids of 4 × 6 traps, five meters apart. The traps were left deactivated during the intervals between trappings and were activated for 48 consecutive hours during each trapping period. To avoid any misleading effects of supplementary feeding, bait was available only during the 48-hour trapping periods. The traps were baited with carrots and standard laboratory mouse pellets (Altromin DK), and checked three times a day. Captured animals were marked individually and released inside the enclosure. If the number of captured voles within a fence exceeded the planned density, surplus voles were released outside the experimental fields. All other small mammals caught occasionally (*Micromys minutus*, *Myodes glareolus*, *Apodemus flavicollis*, *Sorex araneus*, *S. minutus* and *S. caecutiens*) were removed from the enclosures. Of these species, only the bank vole (*M. glareolus*) has the potential to damage tree seedlings, and their proportion in all the animals captured was extremely small; only three bank voles were caught during the experiment, and all those during the first trapping session. Despite efforts to manipulate vole densities by removing surplus individuals and adding others when densities were below the levels planned, actual vole numbers did not conform to the planned abundance patterns. These shortcomings were taken into account in the statistical analysis (*see* below).

## Statistical analyses

Due to difficulties in maintaining the desired vole numbers in the enclosures, the statistical analyses were not run based on the treatment effect. Instead, vole abundance indices based on live-trapping data, which were treated as continuous variables, provided the basis for analyses concerning the effects of the cumulative vole abundance index (mean number of trapped voles in each enclosure during the experiment, calculated as indiv. ha$^{-1}$) and the peak vole abundance index (highest number of trapped voles in an enclosure, calculated as trapped indiv. ha$^{-1}$). We also generated a third continuous variable: adjusted vole abundance; this was an abundance index adjusted to the carrying capacity. The peak vole number observed in each main study area (Jokioinen and Aura) was assigned a value of one, and each vole number below this was calculated by dividing it by the peak vole number. For instance, in Jokioinen the peak abundance was 518 voles ha$^{-1}$ (adjusted abundance = one) and the next was 495 voles ha$^{-1}$ (adjusted abundance: 495/518 = 0.96). These indices were calculated on the basis of minimum numbers alive for each enclosure, and can only be regarded as indices of vole abundance, not as real vole densities.

Due to a strong correlation ($0.52 < r < 0.94$, all $p < 0.001$) between mean, peak and adjusted vole abundances, we could not compare their effects in the same model. We therefore tested the effects of mean, peak and adjusted vole abundances on vole-caused damage in saplings, sapling survival and sapling growth in separate models, and selected the best fitting model on the basis of maximum likelihood scores (more precisely, negative log-likelihood scores with maximum likelihood estimation method) as a measure of lack of fit (Burnham & Anderson 2000). As all candidate models were equally parsimonious, we did not need an information criterion, such as AIC$_c$, that penalizes for additional parameters. In the models selected, the restricted maximum likelihood (REML) estimation method was applied. Denominator degrees of freedom were calculated using the Kenward-Roger technique.

Statistical analyses were performed using the GLIMMIX procedure of the SAS 9.3 statistical software. In the models, 'woody-plant species', 'vole abundance' and their interaction were assigned as fixed explanatory effects. The effects of the fixed variables on the response variables 'vole damage' (damage or no damage) and sapling survival (alive or dead), were tested using generalized linear mixed models (GLMMs) with binomial error distribution and the logit-link function (i.e., these were logistic regressions). Sapling growth as a continuous response variable was analysed using a linear mixed model with a normal error distribution. Sapling growth (GR) was calculated for each sapling using the equation:

$$GR = \ln(\text{final height}) - \ln(\text{initial height}) \quad (1)$$

where, final height was the height measured at the end of the experiment in late autumn of 2003. *Salix myrsinifolia* was excluded from the growth models because of uncertainties in the measurements during the summers of 2002 and 2003. These summers were exceptionally dry and the caps of the *S. myrsinifolia* shoots (five to twenty centimetres) dried out, which may have biased height measurements.

Two random effects were assigned to each model to reflect the spatial arrangement of saplings in the experimental design: 'experimental field' and 'enclosure' (i.e. enclosure/control area) nested within 'experimental field'. The inverse link transform was always applied to request estimates and their precision in the original data scale. The sample size ($n$) in the statistical tests was 1440 (total number of saplings), except in the growth models, from which *S. myrsinifolia* saplings were excluded (*see* above). Although saplings in the growth models totaled 1200, the sample size in these models was 1053 as some measurements were missing.

In order to find a potential threshold vole density, where herbivores expand their diet from the most palatable plants to woody plants, and to determine whether this shift occurs gradually according to the relative palatability of woody species, the number of species damaged by voles was plotted against the mean vole-abundance index. This procedure was performed above the 25% damage level (i.e. 25% of individuals per species damaged by voles). A sigmoidal curve

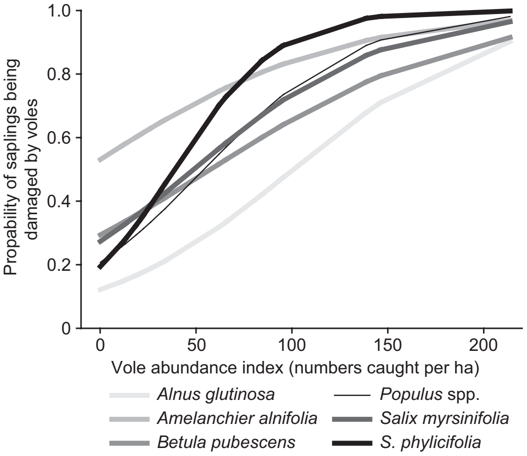

**Fig. 1.** Probability of saplings of six woody-plant species to be damaged by voles, plotted as a function of mean vole-abundance index. Species-specific parameter estimates (intercept and slope) for the interactive term 'species × mean vole abundance' were obtained from the logistic regression model. Original binomial data (damaged or undamaged) are not plotted because of the large number of saplings.

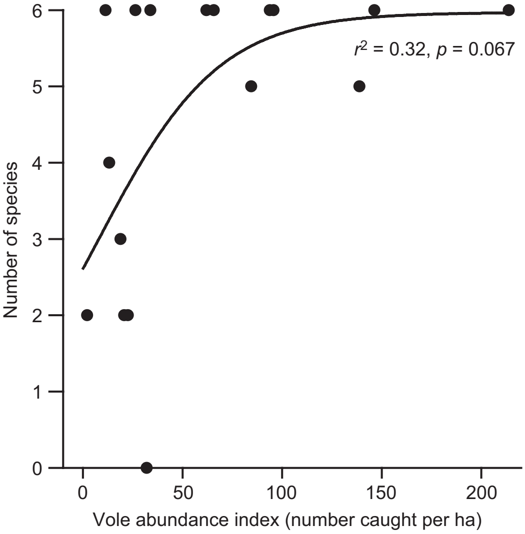

**Fig. 2.** Number of woody-plant species damaged above 25% of their population plotted against mean vole-abundance index. Some saplings in some 'vole exclosures' were damaged by voles although not a single vole was caught during the trapping periods, thus there was some damage at zero abundance.

was fitted and the statistical significance of the non-linear regression was calculated with SigmaPlot ver. 12.0.

## Results

Overall, approximately half (729) of all the saplings (1440) were damaged by voles during the experiment. Comparison of the –2 × log-likelihood of the three vole-abundance models indicated that mean vole abundance and adjusted vole abundance yielded the best fits as an explanatory variables of the probability of being damaged by voles (mean vole abundance: 1297.09 < adjusted vole abundance: 1297.92 < peak vole abundance: 1301.01; mean *vs*. peak vole abundance: $p = 0.048$; mean *vs*. adjusted vole abundance: $p = 0.362$; peak *vs*. adjusted vole abundance: $p = 0.079$), although all three vole-abundance indices significantly explained the probability of vole damage (main effects of mean vole abundance: $F_{1,19.62} = 9.09$, $p = 0.007$; peak vole abundance: $F_{1,18.55} = 6.09$, $p = 0.024$; adjusted vole abundance: $F_{1,18.46} = 8.82$, $p = 0.008$). There were differences between woody-plant species in the probability of suffering vole damage (mean vole abundance × species: $F_{5,\ 1428} = 2.83$, $p = 0.015$; Fig. 1). At low vole abundances, the probablity of *Amelanchier alnifolia* to be damaged was the highest as compared with that of the other species, while that of *Alnus glutinosa* was the lowest, irrespective of vole abundances.

Vole attacks, rather unexpectedly, extended to all six, or at least five, woody-plant species already at low vole abundances (< 50 voles per ha) (Fig. 2). The fitted curve was not satisfactory ($r^2 = 0.32$, $p = 0.067$, Fig. 2). Accordingly, we did not find a clear threshold density, below which the damage would have been limited to the most palatable species only.

The survival probability of all saplings was significantly explained by all vole-abundance indices (Main effects of mean vole abundance: $F_{1,23.56} = 17.10$, $p < 0.001$; peak vole abundance: $F_{1,23.99} = 12.92$, $p = 0.002$; adjusted vole abundance: $F_{1,25.88} = 12.02$, $p = 0.002$). The comparison of the –2 × log-likelihood values of the three models (mean vole abundance: 900.09 < peak vole abundance: 901.40 < adjusted vole abundance: 911.27) indicated that the impacts of peak vole abundance and mean vole abundance did not differ markedly ($p = 0.252$); both peak vole

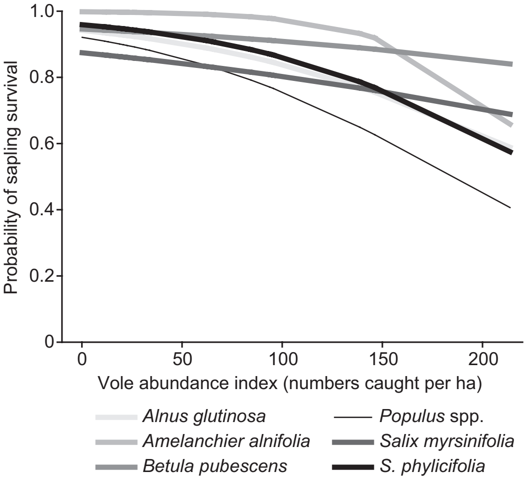

**Fig. 3.** Survival probability of six woody-plant species, plotted against mean vole-abundance index. Species-specific parameter estimates (intercept and slope) for the interactive term 'species × mean vole abundance' were obtained from the logistic regression model. Original binomial data (alive or dead) are not plotted because of the large number of saplings.

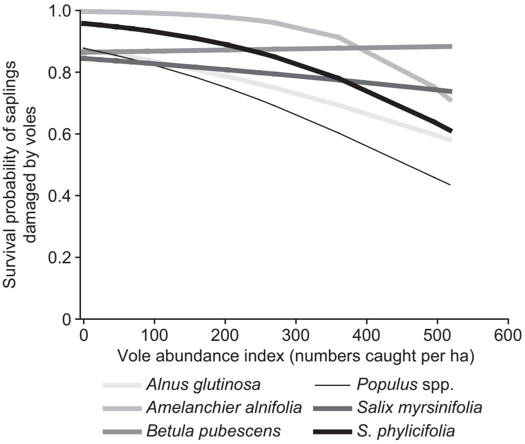

**Fig. 4.** Survival probability of six woody-plant species damaged by voles, plotted against peak vole-abundance index. Species-specific parameter estimates (intercept and slope) for the interactive term 'species × mean vole abundance' were obtained from the logistic regression model. Original binomial data (alive or dead) are not plotted because of the large number of saplings.

abundance ($p = 0.001$) and mean vole abundance ($p < 0.001$), on the other hand, had a better fit than adjusted vole abundance. Sapling survival in relation to increasing mean vole-abundance varied marginally between woody-plant species (mean vole abundance × species: $F_{5,1428} = 2.18$ , $p = 0.055$; Fig. 3).

All vole abundance indices explained the survival probability of saplings damaged by voles (main effects of mean vole abundance: $F_{1,17.44} = 10.58$, $p = 0.005$; peak vole abundance: $F_{1,23.28} = 10.02$, $p = 0.004$; adjusted vole abundance: $F_{1,19.65} = 11.73$, $p = 0.003$). An interactive effect of vole abundance by species was found for peak vole abundance (peak vole abundance × species: $F_{5,717} = 2.27$, $p = 0.046$; Fig. 4) but not for mean or adjusted vole abundances (mean vole abundance × species: $F_{5,717} = 1.93$, $p = 0.088$) adjusted vole abundance × species; $F_{5,717} = 0.93$, $p = 0.463$). A comparison of the –2 × log-likelihood values showed that goodness of fit between the models (peak: 586.72 < mean: 587.93, $p = 0.271$) did not differ, but that both models had a better fit ($p = 0.007$ and $p = 0.014$, respectively) than that with adjusted vole abundance (adjusted vole abundance: 594.00).

Finally, sapling growth was not affected by vole abundance (main effects of mean vole abundance: $F_{1,19.84} = 1.39$; $p = 0.253$; peak vole abundance: $F_{1,20.7} = 0.84$, $p = 0.370$; adjusted vole abundance: $F_{1,17.51} = 0.02$, $p = 0.894$). The –2 × log-likelihood values (mean vole abundance: 861.39 < peak vole abundance: 862.60 < adjusted vole abundance: 869.64) indicated that models with mean and peak abundances as indicators of herbivore abundance did not differ ($p = 0.271$). Both, however, had a better fit than the model with adjusted vole abundance (mean *vs*. adjusted vole abundance: $p = 0.004$; peak *vs*. adjusted vole abundance: $p = 0.008$). Growth pattern in relation to mean vole abundance (mean vole abundance × species: $F_{1,1022} = 2.93$, $p = 0.020$; Fig. 5) and peak vole abundance (peak vole abundance × species: $F_{1,1022} = 2.76$, $p = 0.027$) varied between the species, but growth appeared to follow the same pattern in relation to adjusted vole abundance (adjusted vole abundance × species: $F_{1,1022} = 1.21$, $p = 0.305$.

## Discussion

Contrary to the prediction of the threshold herbivory hypothesis, vole herbivory at low vole

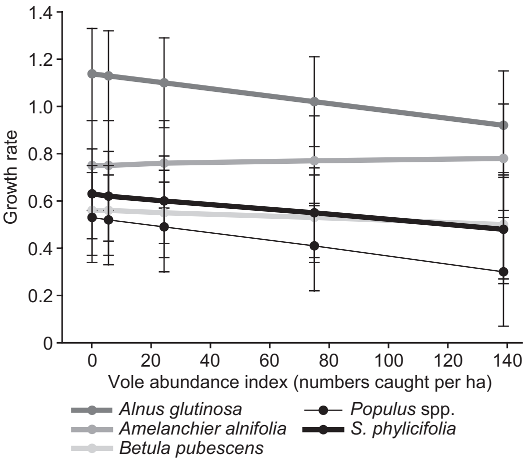

**Fig. 5.** Sapling growth (*see* Eq. 1) of different woody-plant species plotted against mean vole abundance. Dots represent the 10%, 25%, 50%, 75% and 90% percentiles (± 95% confidence limits) of the mean vole-abundance index.

abundances was not limited to the most palatable species. *Alnus glutinosa*, which is perceived as poor forage for voles (Hjälten & Palo 1992, Hjältén *et al.* 1993, Hjältén *et al.* 2004), did not remain intact even at low vole abundances. While the extent of damage varied among species, all species were consumed even at low vole abundances (< 50 indiv. ha$^{-1}$). Furthermore, we did not find consistent evidence for the hypothesis that the top-down effect of herbivores on the establishment of woody plants is more strongly associated with peak abundances than with cumulative herbivory. Cumulative herbivory (mean vole abundance) explained the fate of the saplings equally well or better than did peak herbivory (peak vole abundance). These findings suggest that there is no sharp threshold density above which voles expand their diet from the most palatable plant species to woody-plant species, or that such a threshold lies at very low vole numbers. Our results are in closer agreement with the studies stressing the importance of learning in the food choices of mammalian herbivores (e.g. Bryant *et al.* 1991, Bergvall & Leimar 2005), and with the detoxification limitation hypothesis (Marsh *et al.* 2006). If voles have to learn the suitability of alternative food sources by tasting, vole damage to poor-quality saplings should reflect the cumulative number of individuals, as was in fact the case in our study.

Despite very high peaks in vole abundances in some of the enclosures, most of the saplings in this study survived (88%). Seedling mortality peaks in the early establishment phase, shortly after germination. Previous studies have shown that heavy grazing can cause extremely high mortality (up to over 90%) in woody plants (Gill & Marks 1991, Ostfeld & Canham 1993, Huitu *et al.* 2009). In our study, the saplings were older (1–3 years old), which explains the higher survival as compared with the earlier findings. The proportion of damaged saplings (ca. 50%) was much higher than sapling mortality, suggesting that voles merely tasted most saplings but did not cause fatal damage to them.

Besides seedling or sapling age, the mortality rate of seedlings and saplings attacked by voles is probably affected by the height of the damage to the stem. Prittinen *et al.* (2003) suggested that the mortality of silver birch (*B. pendula*) following field vole herbivory was alleviated by the fact that a majority of the seedlings were cut during seedling dormancy and in such a manner as to leave tall stumps with budst, allowing regrowth. Conversely, the meadow vole, studied in North America (Gill & Marks 1991, Ostfeld & Canham 1993), damages stems at or near ground level or digs up the seedling, which leads to immediate mortality (Prittinen *et al.* 2003). In our experiment, the voles gnawed sapling stems mainly at the height of 1–15 cm above ground. While vole attacks were often fatal to the shoot, parts below the height of one centimeter remained alive and produced new shoots. In the short-term, the survival of damaged saplings may be surprisingly high, as the capacity for regeneration of fast-growing woody species may enable them to overcome even serious damage from herbivores. However, it is also possible that in the long-term the survival of damaged saplings would have been lower; lower height is a disadvantage in the competition for light, and wounds may increase vulnerability to pathogenic infections, which in turn may increase tree mortality after a substantial delay (Gill 1992b, Henttonen *et al.* 1994).

We found considerable among-species variation in survival rates. Surprisingly, *Amelanchier alnifolia* had the highest survival probability, even though the species experienced significant damage already at very low vole abundances. When vole abundance reached 150 indiv. ha$^{-1}$, however, the survival probability of *A. alnifolia* declined sharply. *Amelanchier alnifolia* produced a high number of shoots, so it was probably able to partly compensate for herbivore damage by producing new shoots or reallocating resources to the growth of the remaining shoots.

Vole browsing had a more adverse effect on sapling growth in some species than in others. Most affected were *A. glutinosa*, *Populus* spp. and *S. phylicifolia*, the species that also had the lowest probability of vole damage at low vole densities. Growth varied among species, but this merely reflects differences in the plant's physiology and its capacity to endure given abiotic conditions, rather than the intensity of herbivory. For instance *S. myrsinifolia* saplings suffered severely from drought in the summers of 2002 and 2003, leading to negative average growth both inside and outside vole enclosures.

Interestingly, the top-down effect of vole grazing on saplings was better explained by the indices of actual abundance than the index that had been adjusted to the presumed carrying capacity of the herbaceous vegetation. The experimental fields in Aura were sown with grass seeds at the beginning of the experiment, and manipulations begun before a closed sward developed. In contrast, the experimental fields in Jokioinen were established in grass-dominated vegetation, and abundant cover and food were therefore readily available from the outset. The divergent conditions of the study areas led to major differences in the height of vole peaks, suggesting that carrying capacity of the Aura sites was considerably lower than that of the Jokioinen sites. Despite major differences in apparent carrying capacity, the adjustment of vole abundance indices to the difference in carrying capacity reduced the fit of the statistical model in all analyses. This indicates that the number of voles is more crucial to the fate of saplings than the amount of herbaceous vegetation around the saplings. Our conclusion is in agreement with the previous findings that protective vegetation cover around a sapling increases rather than reduces the risk of sapling damage (Gill & Marks 1991, Ostfeld & Canham 1993, Pusenius & Ostfeld 2000, Pusenius *et al*. 2000).

To conclude, our results did not support the threshold density hypothesis. All woody species were attacked by voles even at low vole abundances, irrespective of their palatability. Yet the most considerable damage (over 60% of saplings damaged per species) was to species more palatable than *A. glutinosa*. While there seems to be no clear threshold, the level of damage thus appeared to vary according to the relative palatability of the plant species in the community. Our results indicate that cumulative herbivory (as indicated by the average number of voles) explains the extent of sapling damage better than peak abundances in vole numbers, or the quantity of herbaceous vegetation providing alternative food and cover. However, the amplitude of the peaks may play a greater role in the severity of sapling damage by increasing the intensity of herbivore attacks, and thereby the mortality of saplings. Saplings appeared to recover well from minor vole damage, suggesting that woody plants have relatively good establishing opportunities even in the presence of voles. High vole densities may, however, reduce growth of saplings, at least at the stand level. Smaller plants are subdominant in the competition for light and space, and the long-term prospects of attacked plants may thus be poorer than is suggested by our experiment, conducted over three growing seasons.

## Acknowledgements

We thank Kyösti Lempa for participation in the planning of the project and Ville Pöyri, Mikko Nieminen, Henrik Heinilä, Sini Kaappola, Taru Kanerva, Jesse Laaksonen, Sami Lyytinen, Sanna Pitkänen and Päivi Sirkiä for assistance in the field. Thanks likewise to Kalle Lertola for statistical advice. We also thank two anonymous reviewers for commenting on an earlier version of the manuscript. The study was funded by the Finnish Academy (KN) and Finnish Cultural Foundation (SG).

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