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The role of phenol-based inducible defense in the interaction between tundra populations of the vole Clethrionomys rufocanus and the dwarf shrub Vaccinium myrtillus

Lauri Oksanen, Tarja Oksanen, Aslak Lukkari and Seija Sirén

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The hypothesis that phenol-based inducible defense has a central role in the dynamics of subarctic vole populations was tested (1) by comparing nitrogen and phenol contents of blueberry twigs from different island and mainland habitats with major differences in the intensity of vole herbivory and (2) by looking at the performance of natural and introduced vole populations and survival rates of blueberry twigs in the mainland and on two islands with heavy vole herbivory in the previous winter. Phenol concentrations were highest on an island without voles and lowest on two intensely grazed islands. Mainland habitats with intermediate intensity of grazing showed intermediate phenol concentrations. Nitrogen concentrations showed a converse pattern, with highest levels on the most intensely grazed islands and lowest ones on the vole-free island. The vole populations on the islands showed annual fluctuations at an exceptionally high level in 1983 and 1984. The performance of the population introduced to a small islet where the blueberry cover had become especially heavily devastated was exceptionally good, both in terms of summer survival and reproduction. In the winter 1983–84, survival rates of voles were fair and did not become improved by provision of supplemental food. Survival rates of blueberry twigs on the islands with dense vole populations were very low. In summer 1984, the vegetation of the densely populated islands was heavily devastated. Yet, the vole population of the main island again reached high densities. The island and mainland populations crashed simultaneously in the winter 1984–85, in spite of major differences in vole density and herbivory between the mainland and the island. These results do not support the idea that phenol-based inducible defense of woody plants would play a major role in the causal mechanism responsible for small mammal cycles in northern Fennoscandia.

L. Oksanen, Dept of Ecological Botany, Univ. of Umeå, S-901 87 Umeå, Sweden. T. Oksanen, Dept of Animal Ecology, Univ. of Umeå, S-901 87 Umeå, Sweden. A. Lukkari, Varpushaukant. 5 B 14, SF-90250 Oulu 25, Finland. S. Sirén, Dept of Biology, Univ. of Turku, SF-20500 Turku, Finland.

Introduction

The apparent abundance of forage in many terrestrial ecosystems has intrigued ecologists for a long time. Hairston et al. (1960, conventionally referred to as HSS) suggested that the world is green because of the regulatory impact of predators upon herbivore populations. The other main explanation states that the greenness of the world does not prevent grazers from being limited by a shortage of adequate resources. Plants are defended and much of the apparent abundance of forage can be inedible (Murdoch 1966) or so high in phenols and low in nitrogen that herbivores attempting to utilize it would end up having negative amino acid balance (Feeny 1975, White 1978).

In this controversy between two schools of population regulation, both can claim theoretical advances and refer to substantial amounts of corroborative evidence.

The hypothesis of inducible defense (Haukioja and Hakala 1975) introduced density-dependence into the conceptual framework of the Murdoch-White hypothesis. Moreover, the mechanism could work with a substantial time delay and thus be a plausible explanation for sustained population cycles (May 1981, Rhoades 1985). Rhoades also complied evidence about changes in plant chemistry attributable to herbivory and documented the widespread occurrence of the phenomenon (but see Fowler and Lawton 1985). In the meantime, Rosenzweig (1973) demonstrated the logical consistency of the HSS hypothesis. A still more recent boost for HSS was provided by reviews of competition experiments (Schoener 1983, 1985).

Also in specific studies on microtines, their food plants and their predators, both schools have gained support. Erlinge (1987) found that exclusion of medium-sized predators dramatically improved winter survival of a vole population in southern Sweden and lead to unusually high vernal population density. On the balance, Oksanen and Oksanen (1981) observed that a decline in a subarctic vole population was accompanied by high concentrations of phenols and low concentrations of nitrogen in the chief forage plant, *Vaccinium myrtillus*. These two pieces of evidence are, however, rather anecdotal. Erlinge's work suffers from lack of replication. Thus, it is impossible to rule out the role of habitat differences between experimental and control plots (Fowler and Lawton 1985). The results obtained by Oksanen and Oksanen can, in turn, represent a mere coincidence between weather conditions favourable for accumulation of phenols and a vole decline caused by entirely different factors (Jonasson et al. 1986, Laine and Henttonen 1987). Ambiguous results which could be used to support both hypotheses were also recently reported by Lindroth and Batzli (1986).

Especially in the case of herbivorous vertebrates, there is a clear need for additional experiments on the role of predation and inducible plant defenses as regulatory factors. Because of formidable technical difficulties in manipulating predator populations, we have started with a test of inducible defense. The study concerns differences between islands on the lake Iešjávri, Norwegian Lapland, and adjacent mainland habitats with large differences in vole densities in 1983 and 1984. We have focussed on the following four predictions of the hypothesis of inducible defense (see Haukioja and Hakala 1975, Haukioja et al. 1983):

(1) Islands and mainland areas where grazing intensity has been very weak should be characterized by higher nitrogen concentrations and lower phenol concentrations in both leaves (summer forage) and green twigs (winter forage) of *Vaccinium myrtillus* than corresponding areas with higher intensity of grazing.

(2) The chemical responses of blueberry twigs to grazing by voles should be accompanied by low survival and/or poor reproductive performance of voles, leading to a population decline.

(3) The decline should not be accompanied by massive habitat destruction or readily observable quantitive shortage of forage (i.e. the world where the voles live shall remain green).

(4) Re-introduction of voles to an island where a crash has recently taken place should fail, unless massive amounts of high-quality food are provided.

The field and laboratory procedures

The index trapping of small mammals in different tundra habitats of Finnmarksvidda, Norwegian Lapland, initiated by Oksanen and Oksanen (1981) in 1977, was continued during 1980–82 on an annual basis (spring indices only). In 1983, when a peak seemed to be approaching, trapping in both spring and autumn was resumed. Islands of the lake Iešjávri were inspected in 1983 to find places where vole densities differed from those on the mainland. The most isolated island in the middle of the lake (Guovdosuolo, referred to below as 'Guovdo') where removal trapping had been performed in 1979 showed no signs of vole activity and yielded no voles with a trapping effort of 148 trap nights. The island was retained as a vole-free control by keeping the 148 snap traps set during 1983–84 (no voles were caught). On another fairly isolated island (Dovtasuolo, referred to below as 'Dovta') trapping (48 trap nights) yielded no voles but both fresh and older signs of winter foraging were abundant. On the largest and least isolated island (Elli-Áslaksuolo, referred to below as 'Aslak'), signs of winter foraging were abundant and grey-sided voles (*Clethrionomys rufocanus*) could be readily observed. (For descriptions of the islands, see Oksanen and Oksanen 1981; notice that Dovta was misnamed there as 'Unnimus'.)

The development of the vole population on Aslak was followed by live trapping on two grids with areas of 1.6 ha (main grid) and 0.8 ha (south grid; the areas include perimeter strips of 5 m). The habitat distributions on the grids were as follows: dry lichen heath 0.3 ha, hummocky lichen heath 0.9 ha (a complex of lichen heath and the next habitat type), cloudberry hummocks 0.4 ha (peat hummocks with luxuriant growth of cloudberry, *Rubus chamaemorus*, blueberry, *Vaccinium myrtillus*, and dwarf birch, *Betula nana*) and open bog 0.9 ha. The two first-mentioned habitat types were restricted to the main grid. Cloudberry hummocks occurred on the south grid only. Open bog occurred on both grids. The two preferred vole habitats (hummocky lichen heath, cloudberry hummocks) occurred as distinct patches, limited by the shoreline or by inferior habitats. The grids were trapped with 'Ugglan special' multiple capture live traps baited with oats. Trapping was performed during 4-day periods with usually three checking rounds per day. The traps were rotated between four stations with distances of 10 m. Four live trapping periods were carried out in 1983, starting 7 July, 19 July, 1 August and 13 September, with traps

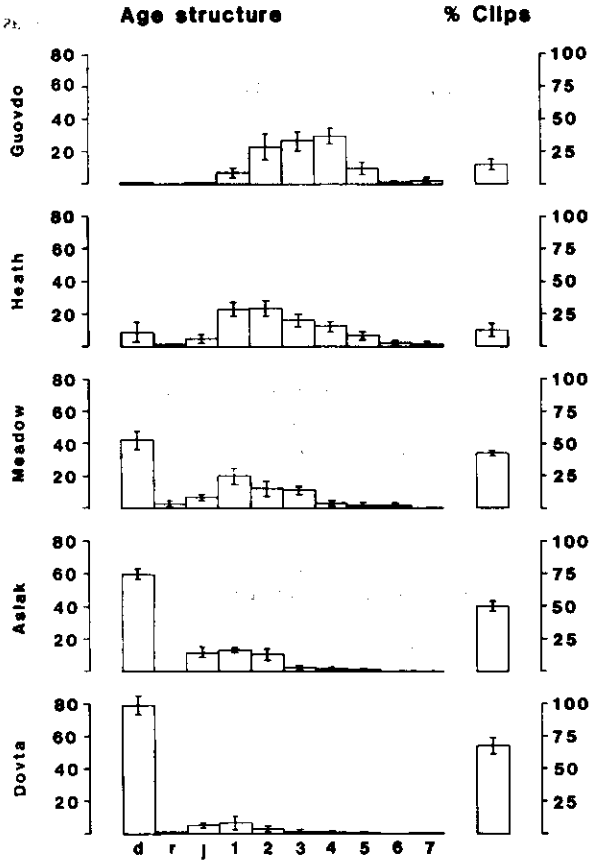

Fig. 1. Age structure of the *Vaccinium myrtillus* populations in mainland heath and meadow and on the three islands in 1983 and percentage of shoot tips ending in a vole clip. Numbers on the x-axis refer to age in years j = juvenile shoots (current year growth only), r = horizontal rhizomes (runners) which have not yet produced above-ground shoots, d = heavily devastated shoots (numbers of clipped-off branches ≥ number of intact shoot tips). Standard errors are indicated by vertical bars.

lying open on the stations between the periods. In 1984, one live trapping period was performed immediately after the breakup, starting 26 June (no pre-baiting). During the night between 25 and 26 August 1984, the western half of the main grid was subjected to 16 h of removal trapping with continuously checked snap traps at intervals of 5 m. In spring 1985, snap-trapping by means of small quadrats was performed in the parts of the grids not affected by the removal trapping (5 small quadrats out of which each represents 24 trap nights).

Four overwintered females and one overwintered male were transferred from Aslak to Dovta 10 July 1983. A live trapping grid covering the entire island (in essence, a 0.2 ha patch of cloudberry hummocks) was established with 10 m intervals between traps. Live-trapping was carried out simultaneously with trapping on Aslak, but with 2 day periods and traps at each station. (Exception: the trapping period starting 24 June 1984 was replaced by removal trapping.) In order to see whether the expected poor survival and reproduction of voles on Dovta (prediction 4) was attributable to lack of adequate forage, we brought 40 kg oats to the island 15 September 1983 and distributed it over the island to places unavailable to birds (spaces between boulders, holes in peat hummocks).

Density estimates of voles for different habitats were based on enumeration within the grids and assignment of voles to the habitat which occupied the largest part of its observed home range during the trapping period. Mature voles captured only once from the edge of the grid were excluded, but other corrections for perimeter error were not made as the preferred habitats had clear limits within the grid or along its edge. During the three trapping periods when traps had been lying on the ground with back doors open before the trapping, there was no reason to correct for variations in trappability, either: almost all mature voles captured from an interior trap station were also recaptured, which suggests fairly complete trapping success. However, during the trapping periods immediately after the breakup, 7 July 1983 and 24 June 1984, rates of recapture were much lower, and several individuals not captured during the first period were trapped later in 1983. Assuming that all overwintered animals present in 1983 had been there during the first trapping period, too, and that survival rates between trapped and untrapped voles were similar, we calculated that the male censuses for 7 July 1983 and 24 June 1984 have to be multiplied by 1.3 and female censuses by 1.6 to make them comparable with the rest of the data.

Blueberry twigs in two mainland habitats (blueberry-lichen heath and herb-grass meadow) were sampled systematically along the perimeters of the vegetation study plots in these habitats by first determining the midpoint of the sampling site with fixed compass directions and then sampling shoots in a widening circle around the midpoint, until a twig sample of 100 g fresh wt was obtained. On Aslak and Dovta, the four most central trap stations of the grids served as centers of blueberry sampling (habitat: hummocky lichen heath on Aslak, cloudberry hummocks on Dovta). On Guovdo, sampling centers were located at 5 m intervals within a narrow strand of hummocky lichen heath. Sampling was performed in the last days of July and first days of August 1983. The numbers of bitten-off branches and shoot tips with current-year segments in each sample were counted. We also age-determined the sampled shoots where at least some branches had all annual segments present. After age determination, rhizomes and non-green above-ground parts were removed. The rest of the treatment was as in the study of Oksanen and Oksanen (1981): preliminary drying in the field, oven-drying (24 h at 80°C) within a week from the sampling, homogenization and determination of nitrogen and phenol concentrations as by Niemelä et al. (1979).

For estimating the intensity of winter grazing in 1983/84, we marked 100 blueberry shoots on each island and in the mainland study areas with strands of plastic

Tab. 1. Phenol and nitrogen concentrations (% dry wt) in blueberry leaves and green shoots in the mainland and island areas sampled in late July 1983.

		Guovdo	heath	meadow	Aslak	Dovta
phenols	shoot	16.4±1.3	15.6±0.5	14.0±0.3	13.1±0.4	11.5±0.3
	leaf	22.2±1.0	19.9±1.0	17.7±0.6	18.5±0.6	16.6±0.9
nitrogen	shoot	0.69±0.08	1.02±0.05	0.97±0.05	0.88±0.09	1.14±0.31
	leaf	1.32±0.11	1.57±0.14	1.95±0.11	1.83±0.20	2.56±0.52

(different colors for shoots without overwintered above-ground segments – juveniles –, for shoots with one overwintered above-ground segment – yearlings – and for older shoots). Marking was performed in August 1983 along transect lines of 1 m, including both depression and hummock sites. In July 1984, we harvested all blueberry shoots within quadrats of 0.8 by 0.8 m around the trap stations of the main grid of Aslak representing the cloudberry hummock part of the hummocky lichen heath complex (12 trap stations; 8 with substantial amounts of blueberry). To obtain a more complete picture on the intensity of winter grazing by voles on the island in 1983/84, we also estimated the coverages of all plants and bare peat on these plots, using an extended Scandinavian coverage class scale (Oksanen 1976). Similar estimations were performed on five reference plots in a corresponding mainland habitat, located using a fixed compass direction and a measuring rope of 15 m.

Results

Structure and chemistry of Vaccinium myrtillus populations

The age structures of the five blueberry populations confirmed our impression of different intensities of winter grazing by voles (Fig. 1). On Dovta, almost the entire blueberry population consisted of recently devastated shoots. This category also dominated on Aslak and on the mainland meadow, whereas older shoots dominated on the mainland heath and especially on Guovdo. On Dovta, clipped-off stubs outnumbered living shoot tips by about 2 to 1 (right part of Fig. 1) which indicates that the power of recovery in the population started to be severely exhausted. On Aslak and on the mainland meadow, the ratio between clipped-off stubs and living tips was about one to one, indicating heavy devastation but also fair recovery. The existence of bitten-off branches on Guovdo was surprising as voles were not caught and typical signs of winter foraging were not observed. The clippings were recent and confined to the youngest segments. In many cases, only a part of current year's growth was removed. This grazing impact was thus recent and probably attributable to a clutch of willow grouse present on the island.

Contrary to the predictions of the hypothesis of inducible defense, the highest phenol concentrations and the lowest concentrations of nitrogen were found on the vole-free and only lightly grazed Guovdo (Tab. 1). The ranking order of the blueberry populations based on increasing phenol contents or decreasing nitrogen contents in leaves matched with the ranking order based on decreasing abundance of devastated shoots. The suggested negative correlation between the level of defense and the intensity of grazing becomes even more clear when the samples are treated individually and the number of bitten-off stubs per 100 living shoot tips is used as an index of grazing (Fig. 2). The correlations between this index and the concentrations of phenols in green shoots (r = −0.82) and leaves (r = −0.72) are negative and clearly significant (p <0.001 in both cases). Nitro-

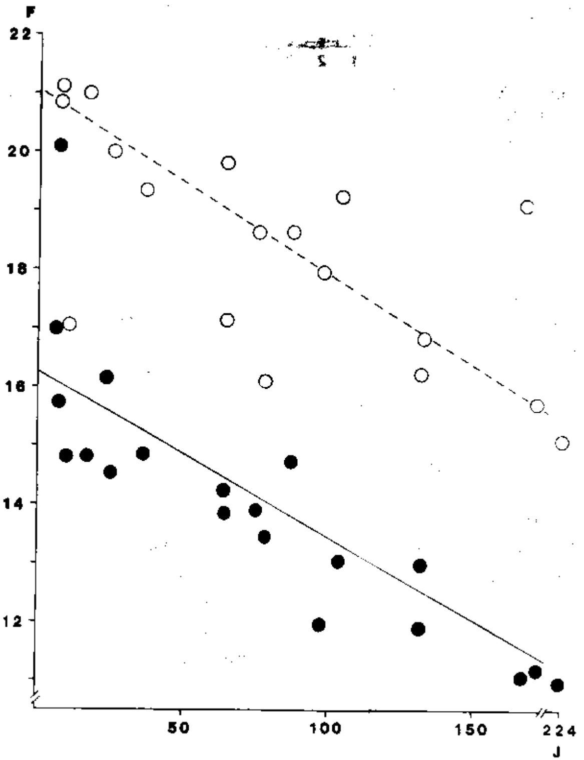

Fig. 2. Relation between the phenol content (F, % dry wt) of green shoots (dots) and leaves (circles) of *Vaccinium myrtillus* and the index of vole grazing (J, number of clipped-off branches/100 intact shoot tips). Solid line = regression line for green shoots; dashed line = regression line for leaves.

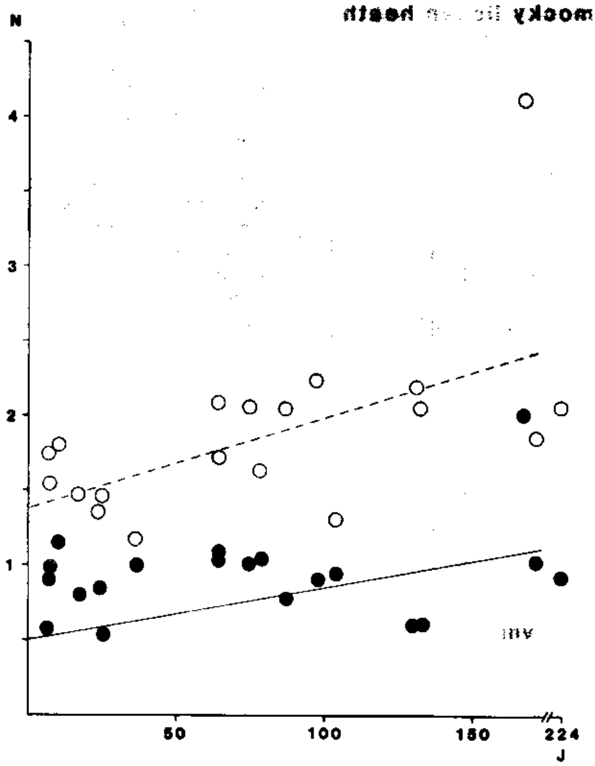

Fig. 3. Relation between the nitrogen content (N, % dry wt) of green shoots (dots) and leaves (circles) of *Vaccinium myrtillus* and the index of vole grazing (J).

gen concentrations are positively correlated with this index of grazing (Fig. 3), although the correlations are weaker ($r = +0.58$, $p < 0.01$ for leaves) and the correlation for green shoots ($r = +0.28$) is not statistically significant.

Population dynamics of Clethrionomys rufocanus on Aslak 1983–84

In spite of substantial intensity of grazing during the winter 1982/83, the vole population of Aslak reached high densities in good vole habitats (hummocky lichen heath, cloudberry hummocks) by autumn 1983 (Fig. 4). The only ominous sign observed was the failure of young voles to mature (only 2 ♀♀ and 1 ♂ were observed to do so). In spite of their failure to mature, however, the age classes of 1983 had fair survival rates during the winter 1983/84, especially in the hummocky lichen heath habitat where even the minimum estimate for winter survival (without correction for the trappability bias) was 14/83 = 0.17. The extremely female-biased sex ratio in June 1984 (23 ♀♀, 1 ♂) suggests that much of the apparent winter mortality was attributable to a factor which affected males much more strongly than females. (There is no reason to suspect a female-biased primary sex ratio: the ten young voles which were mature or close enough to maturation to allow reliable sex determination in September –83, had an even sex ratio (6 ♂♂, 4♀♀).) Winter survival also showed peculiar differences between habitats. The apparently optimal cloudberry hummock habitat seemed to have much lower survival rates than the hummocky lichen heath. (Uncorrected estimates of winter survival, based on the location of home ranges in September 1983, were respectively 2/54 = 0.04 and 14/83 = 0.17 ($\chi^2 = 5.50$, $p < 0.05$).) The hummocky lichen heath habitat occurred in the interior of the island, whereas the pure cloudberry hummock habitat was confined to the southernmost tip of the island, only 800 m from the mainland.

In summer 1984, a new population peak was built up on Aslak (Fig. 4). The evidence for this peak was obtained by a different method which makes detailed comparisons unwarranted. Nevertheless, this new population peak demonstrates that the survivors of the winter 1983/84 were vigorous individuals capable of producing large numbers of progeny, their failure to mature in 1983 notwithstanding.

The population crashed in winter 1984–85; none of the small quadrats trapped in spring 1985 yielded a single vole.

Dynamics of the introduced vole population of Dovta

Out of the five voles transferred to Dovta 7 July, four were still alive by 13 September. The only one which did not survive, perished (together with four juveniles) as a victim of trap mortality. Excluding trap mortality, survival of adults during summer and autumn 1983 was significantly higher (4/4 = 1) on Dovta than on Aslak (10/25 = 0.40; $\chi^2 = 4.97$, $p < 0.05$). Also juveniles survived excellently on Dovta during summer-autumn 1983: the five juveniles which had been marked by 3 August were present 13 September, too. The total number of marked young voles was then 23 (Fig. 5) which gives a production index of 7.7 survived young per female present in late July. The production index significantly exceeded the corresponding index for the same period on Aslak (135/50 = 4.5; $\chi^2 = 5.96$, $p < 0.05$).

On the basis of the excellent performance of the introduced population, high winter survival in 1983/84 was expected, especially as large amounts of high-quality food was provided. However, the apparent winter survival was only 2/27 = 0.07. In addition to the two overwintered and marked voles, we captured two overwintered and unmarked ones and six voles born in late May (age determination on the basis of Viitala 1977). Thus, the reproductive season seems to have continued unusually late in the autumn and started again extremely early in the spring, suggesting that added resources had an impact upon reproduction although not

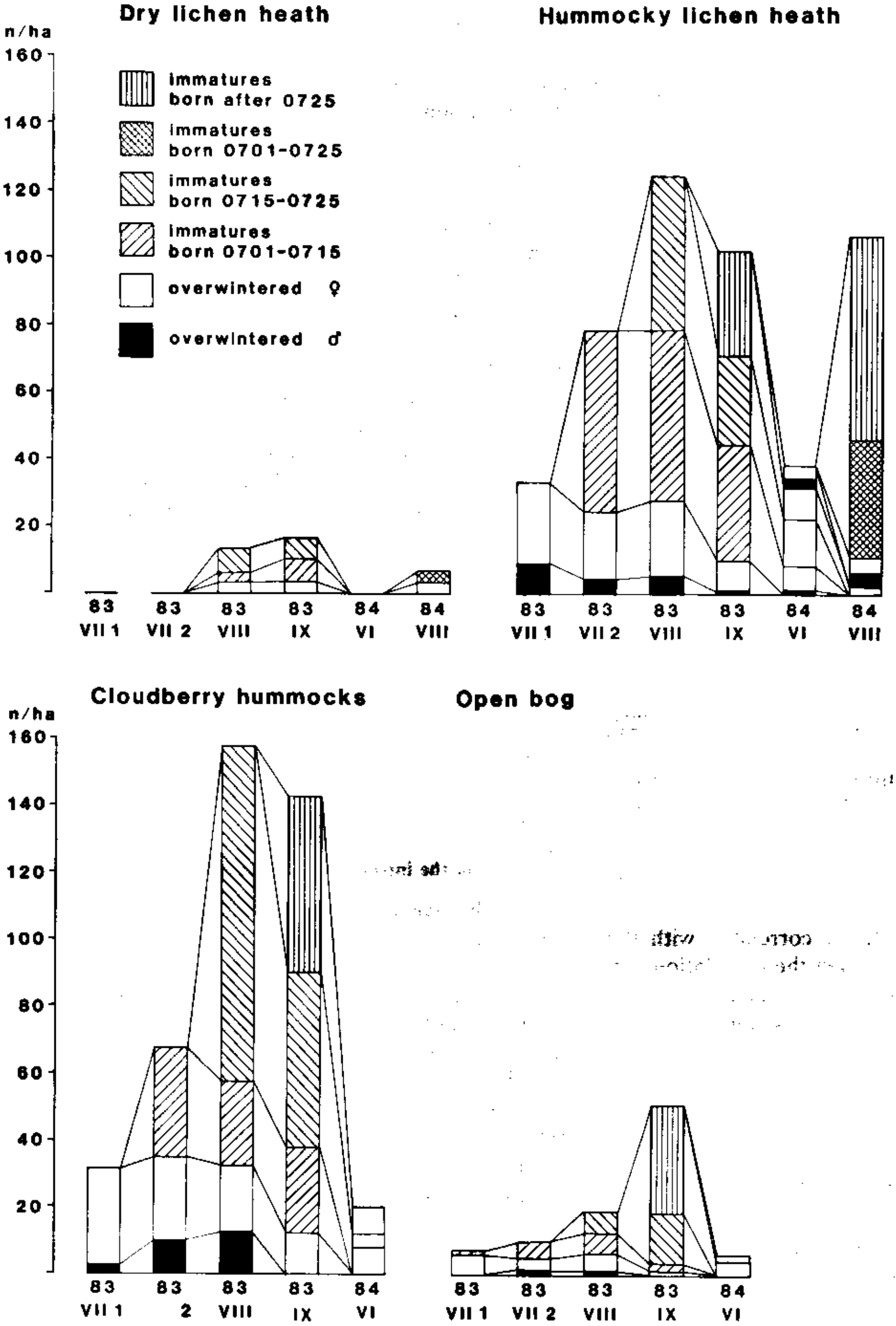

Fig. 4. Estimated abundances of *Clethrionomys rufocanus* (numbers per ha) in different habitats of the island Aslak during the trapping periods of 1983 and 1984 (roman numbers refer to months). Those five voles which were born in 1983 and matured by the September trapping period are included in the category "immatures born 0701–0715" (1–15 July).

on apparent winter survival. The dispersal distance from Dovta to the nearest larger island was 500 m (see Oksanen and Oksanen 1981).

Population trends in mainland habitats in 1982–84

The snap trapping indices for mainland habitats (Tab. 2, see also Oksanen and Ericson 1987: Fig 4) suggest that also mainland populations peaked in 1983–84 but at much lower densities. (Up to a density of about 20 voles per hectare, the indices are comparable to density estimates obtained by live trapping, see Oksanen and Oksanen 1981.) The most striking difference as compared with the islands was a summer decline in 1983 in most mainland habitats. Nevertheless, winter survival in 1983/84 was excellent on the mainland and a population peak was evident in 1984, albeit a weak one in comparison to 1978 (Oksanen and Oksanen 1981).

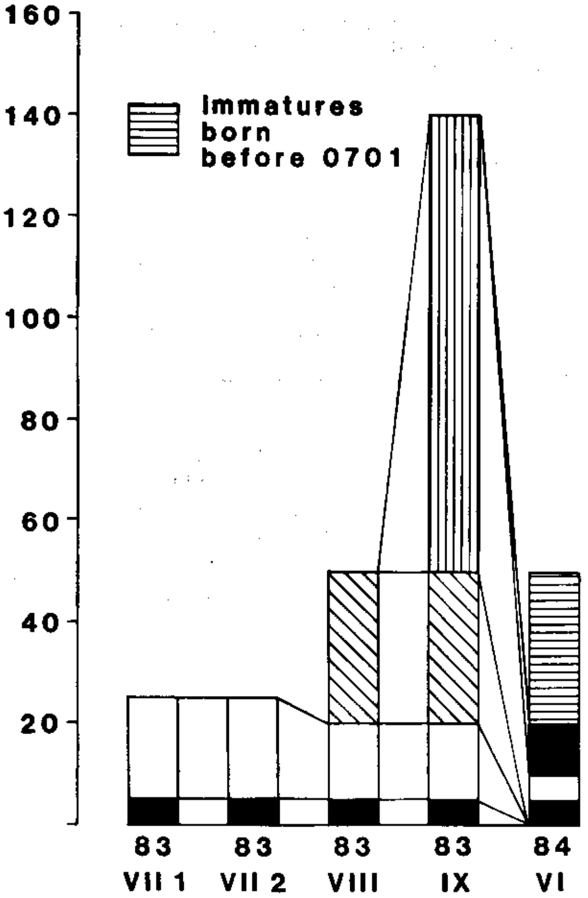

Fig. 5. Estimated abundances of *Clethrionomys rufocanus* on the island Dovta in 1983-84. Symbols as in Fig. 4. Extra food added 15 September 1983.

Vole-blueberry interactions in 1983/84

Winter survival of the marked blueberry twigs varied from excellent on the vole-free Guovdo to virtually nil on Dovta, the ranking order being Dovta <Aslak <meadow <heath <Guovdo (Tab. 3). In the relatively strongly grazed Aslak and meadow populations, yearlings stood out as having clearly higher survival rates than either old shoots ($\chi^2 = 9.24$, $p < 0.01$) or juveniles ($\chi^2 = 16.07$, $p < 0.001$; notice that the juvenile category includes shoots sprouting from clipped-off stubs). In the heath population with relatively low mortality, old shoots survived disproportionately poorly.

The state of the blueberries in June 1984 on the hummocky lichen heath of Aslak (Fig. 6) reflected the low survival in the population. Virtually all shoots belonged to the category 'heavily devastated' and clipped-off stubs outnumbered intact shoot tips, indicating that the power of recovery in the clones started to be exhausted. Coverages of both blueberry (6% ± 2%) and cloudberry (16% ± 4%) were curiously low for this habitat and well below the values obtained from similar mainland habitats (respectively 28% ± 4% and 32% ± 11%). Bare peat, which was only present in trace amounts on the mainland reference plots covered about a third of the habitat (36% ± 8%) on Aslak.

Discussion

An attempt to reconcile the above presented results with the hypothesis of inducible defense appears difficult. If nitrogen and phenol concentrations reflect the level of chemical defense in blueberry twigs and leaves, we must conclude that *Vaccinium myrtillus* responds to grazing by voles by lowering its level of chemical defense. This could have been attributed to successful offensive strategy of the voles (Rhoades 1985) if the relation between the intensity of grazing and the level of defense had been quadratic (i.e. if intermediate levels of grazing had been accompanied by highest levels of defense). However, the trend was a monotonously decreasing one (see Fig. 1) for phenols and monotonously increasing one for nitrogen in leaves (see Fig. 2).

Another possibility is that the induction was missed because we used an inappropriate index of chemical defense. This is conflicted by the bioassays of island habitats performed by the voles themselves. Contrary to predictions (2) and (3), the voles of Aslak did not crash, in spite of widespread habitat destruction, but seemed to obtain a recurrent pattern of seasonal density fluctuations at rather high levels until a simultaneous crash occurred in 1984–85, both in the lightly grazed mainland habitats and on the heavily devastated islands. The fair winter survival in 1983/84 is especially remarkable, because the differences between habitats and sexes suggest that dispersal from the island (probably in May-June when the weather was warm but the lake was still frozen) accounts for a large part of the apparent winter

Tab. 2. Density indices (captures/ 100 trap nights, small quadrat method) of voles in the mainland habitats which either correspond to the island habitats or were represented in the study on *Vaccinium myrtillus*.

	spring 82	spring 83	autumn 83	spring 84	autumn 84	spring 85
Dry lichen heath	0	0.8	0	0	2.5	0
Blueberry-lichen heath	1.7	8.3	7.1	2.5	5.6	0.8
Herb-grass meadow	6.6	12.5	6.5	7.1	10.1	0
Cloudberry hummocks	14.2	11.7	13.3	9.2	23.3	0
Open bog	3.3	2.5	5.0	0	0.8	0

Tab. 3. Survival rates in the marked samples of blueberry shoots during 1983–84 for the entire samples (n = 100), and separately for old shoots (2 years or older in 1983), yearlings (one overwintered above-ground segment in 1983) and young shoots (only current year's growth in 1983). Notice that the last-mentioned category includes both genuine juveniles and recovery shoots, produced by subterranean resting buds of old shoots destroyed by voles. ns = number of survived shoots in 1984, n = number of marked shoots.

Survival		Guovdo	heath	meadow	Aslak	Dovta
over-all	(ns/n = %)	84%	65%	41%	26%	8%
old	ns/n	74/87	18/44	21/58	2/18	2/11
	%	88%	41%	36%	11%	18%
yearling	ns/n	7/10	15/18	8/14	9/16	0/19
	%	70%	83%	57%	56%	0%
young	ns/n	3/3	32/38	12/28	15/66	6/70
	%	100%	84%	43%	23%	9%

mortality. The habitats where most voles disappeared during the winter (cloudberry hummocks, also Dovta with abundance of supplemental food) were those with lowest plausibility of starvation but highest likelihood of dispersal out of the island. Also the disproportionately low persistence of males is more easy to attribute to territorial strife and consequent dispersal (or avian predation) than to starvation. Even prediction (4) failed to match the data. Voles introduced to Dovta did not only survive, but had higher rates of survival and production of surviving young than those left on Aslak.

The results can be reconciled with the Haukioja-Hakala hypothesis of phenol-based inducible defense by assuming that something unusual happened in Norwegian Lapland in 1983–84 which delayed the induction process. (The apparently anomalous situation extended to the taiga of Finnish Lapland, see Henttonen et al. 1987). Such an explanation can be tested by analyzing our blueberry samples from 1984 (the summer preceding the crash). We will do this when some proponent of the induction hypothesis gives firm predictions about the chemical properties of these samples. The hypothesis of Bryant (1981, see also Bryant et al. 1983), according to which the relative unpalatability of shoots with juvenile morphology causes the crash and delays the recovery, is even more difficult to reconcile with current results than the Haukioja-Hakala hypothesis. The supposed cause – heavy prevalence of recovery shoots with juvenile morphology – was observed in 1983 on Aslak and Dovta, but the predicted decline did not take place. Moreover, we got no evidence for the idea that recovery shoots with juvenile morphology would be less preferred than older shoots. The higher survival rates of yearlings suggest that juvenile shoots were actually preferred: both juveniles and yearlings are relatively small and probably harder to find than old shoots. Their chief difference is in the presence of a non-juvenile basal segment in the yearlings.

The current results seem to make it difficult to use the results of Oksanen and Oksanen (1981) as supporting evidence for the induction hypothesis. The observed high phenol/nitrogen ratio in the blueberry samples of 1979 might rather be caused by high July temperatures and extremely low precipitation (Oksanen and Oksanen

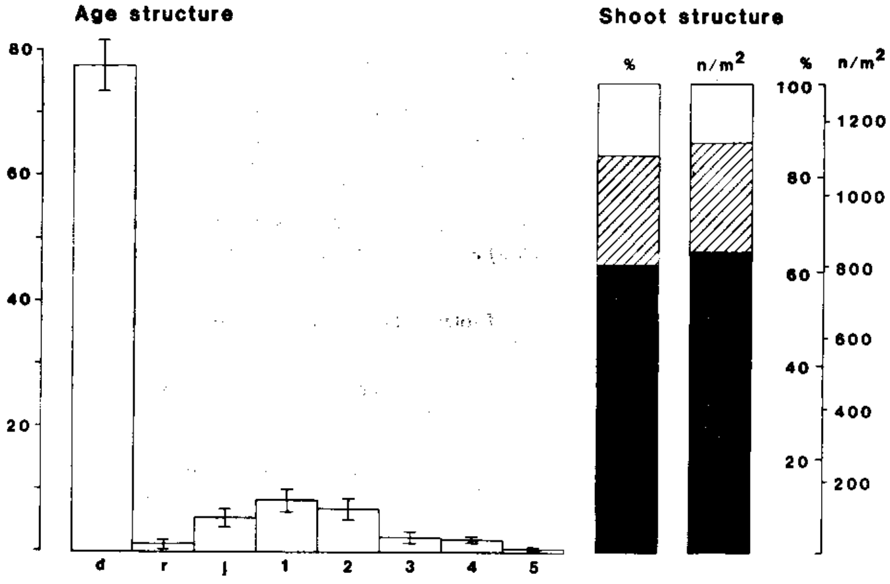

Fig. 6. Age structure and shoot structure of *Vaccinium myrtillus* in the cloudberry hummock habitat of the main study grid of Aslak in 1984. Clipped stubs: black; recovery shoots: hatched; intact branches: white. Proportions of clipped off branches, recovery shoots and intact branches have been calculated both on the basis of proportions (%) and on the basis of absolute numbers (n/m^2) in individual samples.

1981: Fig. 7; see also Jonasson et al. 1986, Laine and Henttonen 1987).

The case of *Clethrionomys rufocanus* and *Vaccinium myrtillus* is not the only one where a woody plant seems to fail to respond to grazing as predicted by the hypothesis of inducible defense. Studies on Scots pine have yielded similar results (Ericson et al. 1980, 1985, Löyttyniemi 1985). Birches seem to respond to grazing by moose by becoming more palatable than unbrowsed birches (Danell et al. 1986) and recovery shoots of heather are preferred by hares (Moss and Hewson 1985). Notice also that the formerly widespread agricultural practice of coppicing would have been disastrous if the juvenile shoots of woody plants which are produced after mechanical damage had low forage quality.

The existence of evidence both against (see above) and for (Rhoades 1985, Haukioja et al. 1985) the induction hypothesis suggests that herbivory can result in vastly different responses in plants. One reason for such differences can be derived from the viewpoint of Moran and Hamilton (1980) by adding the impacts of a short summer to their consideration. With limited time available for folivory, lowered forage quality can indeed be an advantageous response for a plant, because there is little time available for compensating low growth rates by longer developmental time. Thus, herbivorous insects are forced to pupate at lower body weights (Niemelä et al. 1979) and birches seem to gain as individuals (Haukioja et al. 1985). However, reducing growth rates or increasing mortality of a mobile herbivorous vertebrate cannot be favoured by individual selection, because the gains of such an action are spread equally between competing plants. In the interaction between plants and mobile grazers, decreased food quality can only be selected for if it affects the choice of the forager so that a clone with higher level of defense would end up with a larger number of surviving ramets than a clone which has invested the resources in production of new ramets (Moran and Hamilton 1980). In the interaction between voles and the blueberry, this condition is difficult to satisfy, because voles can easily clip shoots at their base and consume those parts which have sufficient quality.

Another factor that tends to create difference is the differences in the effect of folivory and browsing on the carbon-nitrogen balance of the plant (see Tuomi et al. 1984). Folivory deprives the plant of large amounts of nitrogen, thus increasing the degree of nitrogen-limitation and making carbon-based defensive compounds cheap (which, however, does not necessarily imply that inducible defense has a substantial role in population regulation). Browsing which removes large amounts of structural carbohydrates and decimates the numbers of leaf-producing buds should have the opposite effect: the number of leaves which the plant can produce is drastically reduced, carbohydrates are badly needed for the construction of new shoots whereas the rate of nitrogen absorption by the roots is not negatively affected and may be even increased, due to the nitrogen returned to the soil by the herbivores.

The debate whether herbivores are chiefly regulated by inducible defense or predation only applies to habitats where the world seems to be green – i.e. potential forage is abundant. The hummocky tundra with a closed field layer of blueberry, cloudberry and dwarf birch satisfies this condition, as do some other shrubby or herb-rich tundra habitats, but these habitats cover less than 10% of the lowland tundra of Finnmarksvidda and are virtually absent at higher altitudes. The largest part of the tundra is occupied by barren lichen heaths where quantitative food shortage appears to be a plausible limiting factor for voles (Oksanen and Oksanen 1981).

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