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Roe deer *Capreolus capreolus* use of agricultural crops during winter in the Lier valley, Norway

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The quality of common agricultural crops relative to natural plants was measured and the spatial feeding pattern of roe deer *Capreolus capreolus* on strawberry *Fragaria ananassa* fields in the Lier valley, southeastern Norway, were investigated during a winter (1992/93) with shallow snow depth. Strawberry plants were easily digestible, had a high mineral content and were readily harvested by roe deer. Distance to the nearest houses and forest edge affected the spatial pattern of feeding intensity differently when considered at between-field or within-field selection level. Distance to the forest edge had no effect on feeding intensity within fields. Distance to the forest edge had no effect on feeding intensity within fields were close to houses. When fields were far from the forest edge but close to houses, the distance to the houses but not to the forest edge affected within-field use by roe deer. Hence, roe deer seem to assess risk factors (distance to houses) and vary their response to the forest edge accordingly.

Key words: agricultural crops, edge, foraging, plant quality, roe deer

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Winter is a critical period for the survival of smaller cervids at northern latitudes due to increased costs of locomotion and thermoregulation and a concomitant low availability of high-quality forage (Moen 1973, Mautz 1978, Parker, Gillingham, Hanley & Robbins 1996). Concentrate selectors like roe deer *Capreolus capreolus* are adapted to easily digestible forage like herbs (Hofmann 1989), and suffer from severe digestion constraints when forced to feed on typical winter forage like shrubs and browse (Holand 1992, 1994). Nevertheless, roe deer populations have expanded and grown rapidly in Scandinavia during the past century (e.g. Holand & Staaland 1992, Cederlund & Liberg 1995, Wahlström & Liberg 1995). An opportunistic use of the agricultural land-

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scape is a strategy suggested to be partly responsible for this (Holand & Staaland 1992, Cederlund & Liberg 1995). There have been several studies on the use of, and damage to, agricultural crops by the field ecotype roe deer living in large agricultural fields in eastern Europe (Kaluzinski 1982, Obrtel & Holisova 1983, Obrtel, Holisova & Kozena 1984, Holisova, Kozena & Obtrel 1984, Holisova, Obrtel & Kozena 1986), but no study has been conducted in Scandinavian habitats where forests and smaller agricultural fields are interspersed (but see Putman (1986) for England). Neither have any of the studies dealing with the quality of plants eaten by Scandinavian roe deer included agricultural crops (Cederlund & Nyström 1981, Holand 1993). Although damage to crops obviously will increase with increasing roe deer density, we aimed to determine whether agricultural crops are likely to be preferred to other forage, and hence, whether some damage may be expected regardless of roe deer density. Therefore, we measured the quality and potential intake rate (simulated bite per time unit) of common agricultural crops and natural food plants available to roe deer in the Lier valley, southeastern Norway. Furthermore, we provide data on the pattern of use of agricultural fields and test whether risk factors (e.g. Brown 1988, 1992, Lima & Dill 1990) influence the use of fields by comparing feeding intensity within and between fields in relation to distance to human settlements and forest edge.

Study area

The study was conducted in the Lier valley, southeastern Norway (59°45' - 60°00'N and 10°10' - 10° 20'E). The lower part of the Lier valley is dominated by agricultural fields from about 10 to 100 m a.s.l. on rich soil, interspersed with small river valleys bordered with deciduous forest containing species like grey alder Alnus incana, bird cherry Prunus padus, aspen Populus tremula, rowan Sorbus aucuparia and birches Betula pendula and B. pubescens. At both sides of the main valley the terrain rises to more than 500 m a.s.l. and coniferous forest with Norway spruce Picea abies and Scots pine Pinus silvestris dominate. The density of roe deer in the main valley was estimated to be 3-5 deer/100 ha during the study period (Mysterud 1993). Usually, roe deer stay in small family groups of 3-4 deer during winter, but on rare occasions larger groups may form temporarily on agricultural fields (up to 8 in the year of study; Mysterud & Østbye 1997). Red fox Vulpes vulpes is present in the area. In the autumn (August-December) preceding the study period, hunters killed 166 roe deer in the Lier valley, and three deer were shot as pests during the study period (January-March) (Mysterud & Østbye 1997).

Material and methods

Quality and potential intake rate of feeding plants

To get a relative measure of the quality of common agricultural crops relative to natural food plants,

samples of plants were collected within an intensive period in mid-winter. Even within the same plant species, quality probably varies due to differences in shade/light conditions (Bryant, Chapin & Klein 1983, Coley, Bryant & Chapin 1985) and soil. Samples were taken from shaded terrain in cases where the same plant species grew densely in both open and shaded terrain, since shaded terrain is usually preferred by cervids (Hanley, Cates, van Horne & McKendrick 1987, Hieljord, Hövik & Pedersen 1990). The collection of each sample was done applying a technique which imitates roe deer foraging and took place in areas where the plant specimen was considered common. Only plant parts known to be eaten by roe deer were collected (e.g. buds), and only in heights below 1 m, as roe deer usually forage below this height. Foraging efficiency by man was measured for most of the food plants (g dry matter collected per hour) and weight differences between forage types were measured for all the forage plants (g dry matter weight/100 'bites'). At least 45 g dry matter weight of each forage was collected to provide a sufficient sample for all chemical analyses. After collection, the samples were weighed and stored in sealed plastic bags and frozen prior to analysis.

The samples were freeze-dried, ground once through a mill with 1-mm sieve openings and stored in sealed plastic boxes at room temperature. Water content of each forage type was measured by subtracting freeze-dried weight from fresh weight of total forage samples. Pretreatment included cleaning and homogenising of the forage samples (according to procedure 922.02(a) in Helrich 1990). Dry matter content was determined when weight had stabilised after drying at 103°C. The samples were then ashed at 625°C over night, and the ash was dissolved in aqua regia. After evaporation the dry residues were dissolved in hydrocloric acid and diluted appropriately with deionised water. Accurately weighed samples of 2.5 g were dissolved in concentrated HNO₃ (according to procedure 985.01(c) in Helrich 1990), and analysed for Na, K, Mg and Ca. Mineral concentrations were determined by flame atomic absorption spectrophotometry (Perkin-Elmer model 2380). Nitrogen content was determined by Kjeldahl analysis (Tecator, ANN 300) and crude protein calculated as Kjeldahl-N \times 6.25. Total fat (ether-extract) was measured by the Soxhlet method (Tecator, ANS 3414) based on Weende's feed analysis, while the content of hemicellulose, cellulose, lignin and silica were determined by a modified van Soest method

(Tecator, AN 01/78). Total energy content was measured by burning weighed samples of 1 g in an Adiabatic Macrobomb Calorimeter (Gorecki 1975) giving the heat of combustion (net caloric value) of each forage. The mean of two analyses of each forage was used if they differed less than 1% from the average value. Roe deer average digestion capabilities of the different forages were determined using a two stage *in vitro* dry matter disappearance (IVDMD) technique (Tilley & Terry 1963). Rumen liquor from an adult female roe deer shot in the study area during autumn was used. We ran three parallels of each forage.

Feeding intensity variations on strawberry fields

Feeding intensity was estimated on 31 strawberry Fragaria ananassa fields of different age and with different strawberry cultivares. This was done in spring (April) because accumulated feeding is the most important measure for management. The fields were chosen according to damage reports in the region and included fields in which damage had or had not been reported earlier. Strawberry fields were typically separated from each other by forest or often surrounded by other crops, mostly grain fields that were harvested prior to the time of study. Strawberry plants are planted in rows. Estimation of feeding intensity was done by counting the number of bites in four randomly chosen 10-m sections for every 100 m of row in every second row. We occasionally observed feeding by mountain hare Lepus timidus. Feeding by roe deer was easily distinguishable from that of hare through tracks in the snow and the observation that hares only removed strawberry leaves (not the stem).

Statistical analyses

We tested whether the quality of agricultural plants (apple *Malus sylvestris* buds and strawberry leaves) was higher than that of natural plants (pooled) with t-tests. We further tested if: 1) the size of the field, 2) the cultivare of strawberry (Bounty/Corona/Senga/ other), 3) the minimum distance to houses, or 4) the minimum distance to the forest edge could explain why some fields had been visited by roe deer and some had not (logistic regression). Variation in feed-ing intensity among the fields that had been visited by roe deer was tested using multiple ANCOVA. We tested whether differences in feeding intensity within fields could be explained by distance to the nearest

houses or to the forest edge, simultaneously controlling for between-field differences (multiple ANCO-VA). We made separate tests for: 1) fields far (180-400 m) from houses but close to the forest edge, 2) fields situated between the forest edge and houses and 3) fields with medium distance (40-80 m) to the forest edge and short distance (10-20 m) to houses.

Results

Quality and potential intake rate of feeding plants

Agricultural crops had a higher content of Na, Mg, Ca, and K (t-test, N = 24, all P < 0.05) than natural plants pooled (Tables 1 and 2 give more detailed information). There were no differences in hemicellulose and cellulose content of agricultural crops and

Table 1. Content of water (%) and sodium (Na, g/100g), potassium (K, g/100g), calcium (Ca, g/100g), magnesium (Mg, g/100g) and silica (SiO₂, g/kg) in potential roe deer forage plants from the Lier valley, March 1993. Forage types include shoots from four cultivares of apple trees (Lobo, Åkerø, Aroma and Gravenstein) separated into flowering (fl.) and vegetative (vg.) buds, and wintergreen leaves from three cultivares of strawberry plants (Senga, Corona and Bounty). Samples from yew *Taxus baccata* were divided into terminal buds from top (1) and lower branches (2; about 50-100 cm lower than top).

Forage	Water	Na	Κ	Ca	Mg	SiO ₂
Lobo vg.	53.6	0.048	0.62	1.97	0.24	< 0.5
Lobo fl.	53.7	0.036	0.70	2.55	0.21	1.0
Åkerø vg.	52.5	0.023	0.66	1.27	0.20	< 0.5
Åkerø fl.	52.2	0.022	0.69	1.96	0.18	< 0.5
Aroma vg.	50.4	0.043	0.65	1.82	0.24	< 0.5
Aroma fl.	49.3	0.027	0.67	3.25	0.13	< 0.5
Gravenstein vg.	57.5	0.041	0.91	1.98	0.31	< 0.5
Gravenstein fl.	56.0	0.028	0.81	2.25	0.27	< 0.5
Senga	43.5	0.027	1.31	0.67	0.27	2
Corona	54.6	0.014	1.00	0.91	0.27	< 0.5
Bounty	47.4	0.021	1.17	1.09	0.26	< 0.5
Avena sativa	51.6	0.011	0.19	0.13	0.06	2.0
Vaccinium myrtillus	59.9	0.014	0.41	0.51	0.08	< 0.5
Calluna vulgaris	63.4	0.015	0.37	0.36	0.13	< 0.5
Vaccinium vitis-idaea	46.4	0.008	0.48	0.55	0.13	<0.5
Sorbus aucuparia	54.2	0.013	0.52	1.20	0.24	< 0.5
Betula spp.	47.6	0.012	0.33	0.72	0.13	< 0.5
Populus tremula	39.9	0.017	0.41	1.20	0.16	< 0.5
Salix caprea	51.0	0.027	0.53	1.42	0.14	< 0.5
Fraxinus excelsior	38.4	0.012	0.79	1.01	0.16	< 0.5
Prunus padus	55.1	0.013	0.61	1.65	0.16	< 0.5
Corylus avellana	55.2	0.013	0.54	0.87	0.21	< 0.5
Acer platanoides	54.8	0.013	0.71	1.10	0.12	< 0.5
Alnus incana	48.3	0.014	0.42	0.55	0.11	< 0.5
Pinus silvestris	50.2	0.017	0.50	0.26	0.09	< 0.5
Picea abies	46.6	0.008	0.65	0.45	0.09	< 0.5
Juniperus communis	53.5	0.014	0.44	1.27	0.13	< 0.5
Taxus baccata (1)	51.2	0.008	0.95	0.79	0.16	< 0.5
Taxus baccata (2)	60.2	0.007	0.81	1.27	0.13	< 0.5

Table 2. Content of hemicellulose (Hemi.), cellulose (Cell.), lignin, protein, ether-extract (g/100g dry matter) and total energy (kJ/g dry matter) in potential roe deer forage plants from the Lier valley, March 1993. The *in vitro* dry matter disappearance (IVDMD - % digested of total dry matter mass) is based on results from only one animal shot during autumn.

Forage	Hemi.	Cell.	Lignin	Protein	Ether-extract	Total energy	IVDMD ± sd
Lobo vg.	11.43	16.27	9.58	8.69	7.57	19.560	56.3 ± 9.0
Lobo fl.	8.35	11.69	8.77	10.44	10.04	19.861	65.0 ± 4.2
Åkerø vg.	14.87	16.61	7.08	8.75	7.25	19.362	70.7 ± 8.3
Åkerø fl.	10.14	13.83	8.91	11.44	9.58	19.810	62.2 ± 4.6
Aroma vg.	14.08	16.24	6.99	9.44	6.06	19.283	74.5 ± 4.6
Aroma fl.	8.28	12.47	10.12	11.87	8.30	19.065	73.7 ± 2.0
Gravenstein vg.	11.69	10.77	6.56	9.75	6.71	19.120	65.4 ± 8.7
Gravenstein fl.	9.02	14.34	8.50	10.62	9.05	19.355	70.2 ± 4.2
Senga	8.57	11.15	3.10	12.37	3.23	19.004	84.8 ± 4.0
Corona	8.06	7.95	2.89	13.00	3.23	18.891	86.7 ± 3.5
Bounty	9.41	9.82	2.69	11.62	3.43	18.794	76.6 ± 0.0
Avena sativa	32.02	23.11	1.45	6.81	1.38	19.192	66.4 ± 7.2
Vaccinium myrtillus	10.26	16.68	13.99	7.87	2.79	20.916	59.1 ± 1.2
Calluna vulgaris	18.74	13.66	13.35	8.00	5.66	20.991	49.8 ± 4.6
Vaccinium vitis-idaea	11.69	10.10	7.54	6.56	6.15	21.679	51.3 ± 4.2
Sorbus aucuparia	8.24	19.05	6.28	9.56	7.80	20.194	68.3 ± 8.3
Betula spp.	12.12	10.67	19.48	9.56	17.82	24.256	44.4 ± 4.0
Populus tremula	13.75	15.99	26.88	7.56	12.98	21.802	46.1 ± 6.0
Salix caprea	11.68	17.42	11.07	9.56	6.50	20.914	53.5 ± 7.2
Fraxinus excelsior	10.86	9.84	6.76	9.37	3.79	19.583	
Prunus padus	12.14	13.07	14.83	15.69	4.01	19.956	
Corylus avellana	15.42	17.85	8.24	11.00	3.72	20.703	40.6 ± 17.0
Acer platanoides	7.09	9.25	4.11	9.94	6.88	19.514	
Alnus incana	10.15	8.67	9.51	12.37	24.92	24.926	30.5 ± 7.1
Pinus silvestris	14.84	24.89	11.05	8.06	9.04	21.687	40.8 ± 3.1
Picea abies	15.10	20.35	12.25	8.06	5.67	20.281	44.3 ± 9.0
Juniperus communis	9.75	17.30	12.37	7.75	12.67	21.815	51.3 ± 2.0
Taxus baccata 1)	7.31	8.26	9.85	13.44	7.42	20.213	73.0 ± 4.2
Taxus baccata 2)	7.54	7.75	10.83	10.19	9.33	20.856	76.8 ± 5.8

natural forage, whereas agricultural plants had a lower lignin content, a higher content of crude protein and a higher IVDMD than natural plants (all P < 0.005). The content of ether extract was similar (P =

0.256), although strawberry had a low content of ether extract (see Table 2). Strawberry leaves also had a high potential intake rate (Figs. 1 and 2). There was little variation in chemical content and potential



Figure 1. Potential intake rate measured as g dry matter/hour for some of the most common forage types available to roe deer in the Lier valley, Norway.



Figure 2. Dry matter weight of 100 collected 'bites' of the forage types available to roe deer in the Lier valley, Norway.

intake rate between different cultivares of strawberry (Corona, Senga and Bounty) and buds (vegetative and flowering) of apple trees.

Feeding intensity variations between strawberry fields

Roe deer were more prone to feeding on small fields than on larger fields (logistic regression, N = 31, P =0.019), but neither cultivare of strawberry (P = 0.265-(0.993), distance to forest edge (P = (0.354)) nor distance to human settlement (P = 0.967) affected choice of field. The number of available strawberry plants per field varied between 1,620 and 38,220 (i.e. field size between 0.034 and 0.805 ha), the minimum distance to cover between 0 and 120 m and distance to human settlement between 10 and 300 m. No differences were found in feeding intensity (0.01-11.01 bites/10 m of transect) among the fields visited (multiple ANCOVA, N = 19, $r^2 = 0.348$) due to cultivare of strawberry (F-ratio 1.777, P = 0.205), field size (F-ratio 0.271, P = 0.612), distance to forest edge (F-ratio 0.218, P = 0.649) or human settlement (Fratio 0.053, P = 0.821).

Feeding intensity variations within strawberry fields

Feeding intensity within strawberry fields far from

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houses but close to cover (3 fields, multiple ANCO-VA, N = 80, $r^2 = 0.128$), controlling for variation between fields (F-ratio 3.342, P = 0.041), did not vary with distance to the nearest house (F-ratio 2.578, P = 0.113) nor with minimum distance to the forest edge (F-ratio 1.483, P = 0.227). Feeding intensity within fields situated between the forest edge and houses (12 fields, multiple ANCOVA, N = 338, r^2 = 0.747), controlling for variation between fields (Fratio 77.061, P = 0.000), decreased with increasing distance to cover (F-ratio 48.450, P = 0.000), but there was no effect of distance to the nearest house (F-ratio 0.056, P = 0.813). Feeding intensity in fields situated between two houses and with medium distance to the forest edge (3 fields, multiple ANCOVA, N = 106, $r^2 = 0.552$), controlling for variations between fields (F-ratio 6.176, P = 0.003), increased with increasing distance to the nearest house (F-ratio 115.688, P = 0.000), but was not related to distance to the forest edge (F-ratio 0.057, P = 0.813).

Discussion

Wild northern ruminant diets are usually low in essential minerals like Na, Cl and P, and the balance of mineral metabolism is usually marginal (e.g. Holand & Staaland 1995). Roe deer usually have effective mechanisms to maintain high gastrointestinal concentrations of minerals by recirculating endogenous pools (Holand & Staaland 1995). Within the constraints set by predation risk, thermal comfort, and social interactions (Hjeljord, Sæther & Andersen 1994), ruminants are usually regarded as energymaximisers during winter in an optimal foraging framework (Schoener 1971, Belovsky 1981, Schmitz 1991), but in some cases energy-maximation must be balanced against sodium intake (Belovsky 1986, Forchhammer & Boomsma 1995). This is also evident from white-tailed deer Odocoileus virginianus use of mineral licks, where sodium is the primary mineral sought (Kennedy, Jenks, Jones & Jenkins 1995). It is evident from the chemical content analysis that strawberry plants and apple-buds should be preferred to most of the natural plant species in terms of digestible energy (high N and IVDMD, low lignin content) and mineral content. Strawberry most likely also has low quantities of tannins and terpenes, potentially limiting intake because the ether extract part was low (McDonald, Edwards & Greenhalgh 1973, Schwartz, Nagy & Regelin 1980) and since they have not been exposed to heavy browsing pressure during recent evolutionary time.

It has been shown that ruminants prefer forages which are readily harvested (Kenney & Black 1984). Using data based on people simulating roe deer feeding, our study shows that strawberry plants are far more easy to harvest than most other food plants. Some of the strawberry fields have such large quantities of forage that the marginal value (Charnov 1976) of energy gain in agricultural fields probably does not drop below the average of other habitat patches. We suggest that three factors may potentially prevent roe deer from a greater utilisation of agricultural fields:

 Ruminants prefer high-energy food like grain, but they limit intake of grain and increase intake of alternative foods once grain is overingested (Provenza 1995). The decrease in intake is due to postingestive malaise evidently caused by an excess of byproducts from microbial fermentation (Provenza, Ortega-Reyes, Scott, Lynch & Burritt 1994). Therefore, it seems likely that varied diets are a result of the costs rather than the benefits associated with high intake of one plant (Provenza 1995, 1996). However, ears of rye and wheat constituted more than 90% of the total dietary biomass of Polish field living roe deer (Kaluzinski 1982). Thus, roe deer are obviously able to live almost exclusively on agricultural crops if they have to.

- 2) Habitat selection often reflects foraging situations in which animals experience a trade-off between foraging and exposure to predation (Milinski & Heller 1978, Sih 1980, review in Lima & Dill 1990). Foraging deer use open habitat more often at night (Selås, Bjar, Betten, Tjeldflaat & Hjeljord 1991) and often prefer to feed close to cover (Keay & Peek 1980). There was no effect of distance to forest edge on the choice of field (see below), suggesting that risk factors were not strong enough to prevent roe deer from feeding on fields if within their home range, although it may influence the time spent in the patch (Brown 1988).
- 3) Agricultural fields are also climatically exposed. However, studies on white-tailed deer indicate that when feeding on high energy forage, costs of thermoregulation are minor compared to benefits gained through foraging (Moen 1968). Thermal factors are therefore probably of less importance than mixed diets and risk factors.

Spatial variation in feeding patterns

The spatial feeding pattern on agricultural fields with regard to distance to the forest edge was different at the between-field and within-field selection levels, supporting the importance of spatial scaling in ecology (Senft, Coughenour, Bailey, Rittenhouse, Scala & Swift 1987, Morris 1987, Orians & Wittenberger 1991). We detected no effect of distance to houses or forest edge on the choice of fields, but the largest fields were avoided. Although small variations in these parameters may explain some of our results, a seemingly random element in which fields are visited or not is in accordance with studies on whitetailed deer (Conover 1989). Some fields seem to suffer extensive damage while other fields close by are not fed on at all even though the fields look similar (Conover 1989).

The spatial variation in feeding intensity within fields showed large variation among fields. There were no effects of distance to either houses or forest edge when fields were situated far from houses but close to the forest edge. When fields were situated between houses and the forest edge, feeding intensity decreased with increasing distance to forest edge, whereas distance to houses was important for fields situated between houses but with a medium distance to the forest edge. This highly variable behaviour to forest edge may explain some of the contradiction among studies showing increased use of areas close to cover (Keay & Peek 1980, Hansson 1994) compared to those showing no such response among cervids (Kirchhoff & Schoener 1983, Andrén & Angelstam 1993). Definitions of forest edge may also influence the results (Kremsater & Bunnell 1992). Roe deer seem to assess risk factors (i.e. distance to houses) and vary their responses to forest edge accordingly.

Temporal variation in feeding patterns

Damage due to browsing by roe deer on strawberry plants and apple orchards has been observed and reported in local newspapers as long back as 1943 and 1944 (Anonymous 1943, 1944). This took place long before roe deer reached their present high population densities in Scandinavia (Wahlström & Liberg 1995), and is in accordance with our findings that strawberry plants represent high-quality forage and hence are selected, regardless of roe deer density, although the total level of damage is likely to increase with increasing roe deer density. Regardless of density, it is likely that there will be considerable yearly variations in the feeding intensity by roe deer on agricultural crops. Roe deer typically forage less in the field layer and more in the bush layer with increasing snow depth (Cederlund, Ljungqvist, Markgren & Stålfelt 1980, Mysterud & Østbye 1995, but see Mysterud, Bjørnsen & Østbye 1997). During periods with deep snow, the accessibility of apple buds and browse will increase relative to bilberry and strawberry. However, the search costs in all open terrain (e.g. apple orchards) will also increase, so these issues clearly need further study.

Management implications

Not all feeding on crops result in plant production loss. The level of production loss will vary with the time of growth during which feeding occurs and also with what part of the plant the animal consumes (Diekmann 1983). Most of the feeding on strawberry plants should not severely affect plant production, since roe deer often eat leaves that are damaged by the cold during winter and would have been replaced anyway. However, severe damage occurs when feeding starts during autumn, before young plants develop a root-system deep enough to avoid being pulled out of the ground. Furthermore, trampling may destroy the small fruitbearing buds in late winter and early spring, and also the plastic coverage in which the plants are embedded (Mysterud & Østbye 1997). Damage to apple farms is probably a more severe problem, and farmers have reported large damage to 22% of the apple orchards in the Lier valley (Mysterud & Østbye 1997). Conover (1989) found that when 20% of apple buds were eaten, there was a production loss of 20%. In good years, there are too many flower buds on apple trees and farmers usually have to remove some. Hence, in these years feeding will not result in production loss, but will actually lighten the work load of the farmer. Foraging on vegetative buds may, on the other hand, retard the growth and deform the shape of the apple trees. Furthermore, breakage of twigs of young trees may be a problem with the most recently favoured growth form in Norwegian apple orchards (called 'myk spindel') which gives low and broad shaped apple trees.

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