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Feeding Ecology of Roe Deer, *Capreolus capreolus* L., during summer in southeastern Norway

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Ten radiocollared Roe deer were followed over three summers, resulting in 2316 map locations. The animals utilized a mixture of forest and agricultural land. Cover and forage availability were the main determinants of habitat selection. Forest plantations on rich sites were the most preferred habitat. Open habitats like meadows were used mostly at night. Grain-fields were avoided. The animals fed on a variety of forbs and browse species, particularly wood anemone (*Anemone nemorosa* L.) in early spring, and meadosweet (*Filipendula ulmaria* L.) throughout the summer. Browsing increased from early to late summer. This coincided with a change in the feeding-resting rhythm, indicating a decrease in overall forage quality. Carrying capacity of the study area is discussed in relation to quality of summer habitat.

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INTRODUCTION

Roe deer *Capreolus capreolus* (L.) have a wide distribution in Scandinavia and occur today from southern Denmark and Sweden to the northernmost counties in Norway (Huseby 1989). Range-animal interactions may be expected to vary with variations in habitat and climatic conditions, but this has not been studied extensively in Scandinavia.

Strandgaard (1972) investigated Roe deer on the east coast of Denmark in a mixture of farmland and deciduous/coniferous forest and found that the animals fed on agricultural land during summer and fall and moved into the forest during winter. The only other studies of feeding ecology and habitat preference of Roe deer in Scandinavia were done by Cederlund et al. (1980) and Cederlund (1983) in inland coniferous forests in mid-Sweden. Here Roe deer showed a clear preference for particular forage plants, but a consistent preference for particular forest types could not be detected, although open areas like clear-cuts and bogs were avoided. Cederlund (1983) concluded that further progress on this subject would require other definitions of habitat types combined with more detailed analyses of the range.

Presently, therefore, we lack basic knowledge of Roe deer range ecology in Scandinavia. Such information is fundamental in understanding the influence of modern forestry and agriculture on Roe deer habitat. In this study we investigated Roe deer use of forest and agricultural areas during summer in southeastern Norway. We also gathered data on forage preference and activity in relation to season. The data were collected from radiocollared animals.

STUDY AREA

The 2 km^2 study area is located on the property of the Norwegian Agricultural University at Ås (59° 41' N, 10° 47' E), about 15 km from the coast. The climate is semi-continental and the ground is usually snow-covered from early January to mid-April, reaching a maximum depth of approximately 50 cm in March. The mature forests, mainly spruce (*Picea abies* L.), are harvested by clear cutting. Birch (*Betula* spp.), rowan (*Sorbus au-*

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cuparia L.) and aspen (*Populus tremula* L.) dominate the first years after cutting. Forest covers approximately 61% of the study area and is interspersed with grain fields and pastures. The study area was divided into habitat units depending on site quality and height of trees. Vegetation of the field layer was used as an indication of site quality according to the system of Hesjedal (1973). Hesjedal's vegetation types (given by letters below) were combined into five site quality classes: 1) poor (A2, A3, B2, G3, ca. 40% of the forest), 2) medium (B3, C2, C3, ca. 40% of the forest), 3) good (B4, C4, ca. 15% of the forest), 4) rich (E3, ca. 5% of the forest), 5) meadows (R3, S1, S2, ca. 1% of the study area). We also distinguished a class 6), grainfields (38% of the study area). Height of conifers (h) was used to classify forest stands: 1) clearcuts, poor coverage (h <0.5 m, ca. 8% of the forest, 2) plantations, good coverage (h = 0.6—3 m, ca. 25% of the forest), 3) young forest, very good coverage (h = 3.1—8 m, ca. 6% of the forest) and 4) older forest, coverage variable (h >8.1 m, ca. 61% of the forest).

METHODS

Roe deer were trapped and radio-collared within the study area, and animal positions were determined by triangulation using a handheld antenna and a compass (see Bjar et al. (1991) for a description of equipment and methods). During 1984—86 we obtained 2319 locations from 10 different animals. Twenty-two percent of the recordings were obtained between 2100 and 0600 hours. During the summers of 1984 and 1985 animal locations were plotted once or twice during every 48-hour period. During 1986 the animals were located once an hour for eight 24 hrs periods spread evenly over the summer (May—September). Whether animals were active or not was judged from evenness of signals. By comparing signals with direct observations of radio-equipped animals it was possible to distinguish patterns indicating rest and movement.

Feeding on plant species of the field layer was recorded within the areas with the most locations each month. A total of 186 plots (1 x 1 m) were located where fresh feeding signs (plants tissue removed) were detected. The number of bites on each plant species was counted. A preference index was obtained by dividing the number of bites on a species by the horizontal coverage (%) of that species. An index of utilization for various browse species over the summer was obtained along randomly placed survey lines. Biomass removed from browsed trees was estimated by comparing the number of leaves completely or partly eaten with the total number of leaves on the tree. The method did not allow comparison on a quantitative basis between browse feeding and feeding on plants of the field layer. There were no moose (*Alces alces* L.) in the area and hares (*Lepus timidus* L.) were rare.

Boundaries of animal home ranges were determined according to the method of Harvey and Barbour (1965), as modified by Wegge and Larsen (1987). Habitat preferences were determined on all home ranges combined. The number of plots on each habitat type was divided by the total area of the type within the home ranges and the resulting ratio was the measurement of preference. Habitat preferences were further investigated by dividing the forest within the study area into 50 x 50 m squares and randomly selecting 10 squares among those with no or only one animal location. These were compared with the ten squares with the highest number of locations. The vegetation on each of the 20 squares was investigated on random plots using standard plots of 50 m^2 (Landsskogtakseringen 1970).

RESULTS

Of 158 plant species recorded on feeding plots, 96 were fed on by Roe deer; on 50 of these we counted more than 10 bites over the summer. Meadowsweet (*Filipendula ulmaria* L.) was important in the diet throughout the summer, except during early spring when wood anemone (*Anemone nemorosa* L.) appeared to be the only species fed on. Other species occurred in the diet during definite periods (Fig. 1).

The most preferred forage plant was giant bellflower (*Campanula latifolia* L.), followed by rosebay willowherb (*Chamaenerion angustifolium* L.), lesser celandine (*Ranunculus ficaria* L.), dandelion (*Taraxacum cordatum* l.), and marsh marigold (*Caltha palustris* L.) (Table 1). The difference in preference was significant between giant bellflower/rosebay willowherb and the other spe-

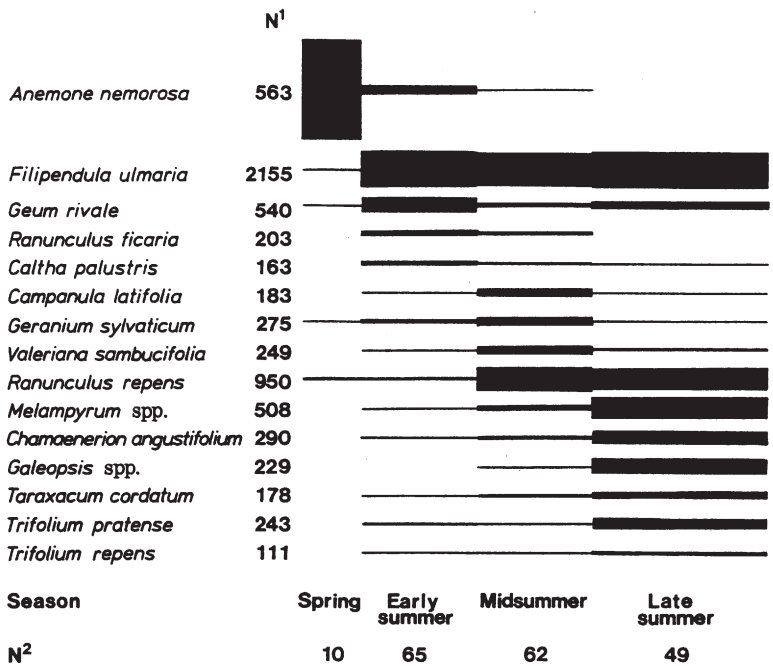

Fig. 1. The most important plant species of the field layer fed on by Roe deer during summer at Ås. Height of bars indicate importance of species (average number of bites per plot). N^1 = Total number of bites on each plant species over the summer. Season = spring: 1.5—15.5, early summer 16.5—15.6, mid-summer: 16.6—15.7, late summer: 16.7—1.9. N^2 = number of sample plots during each period.

cies (Kruskal-Wallis; $p<0.05$). Among closely related species, red clover (*Trifolium pratense* L.) was preferred over white clover (*Trifolium repens* L.) (Kruskal-Wallis; $p<0.05$). The influence of abundance (coverage) on preference was tested for meadowsweet, but no significant relationship was found (Kruskal-Wallis; $p>0.05$). Among browse species, rowan was the species most often fed on, followed by great willow (*Salix caprea* L.). Oak (*Quercus robur* L.), aspen, maple (*Acer platanoides* L.) and ash (*Fraxinus excelsior* L.) were not much eaten. Birch was intermediate. The majority of browsing occurred on plantations, where animals fed on fresh leaves of stump shoots and root suckers. Feeding in the brush layer increased over the summer. The average biomass of leaves removed from browsed trees in June was 21.5%, in July 43.5% and in August 48.1%. The difference was significant between June and August ($X^2 = 39,9$, $p<0.005$).

Importance of forage plants of the field layer differed with site quality. On poor sites common cow-wheat (*Melampyrum pratense* L.) dominated the diet, while on medium sites rosebay willowherb, common cow-wheat, and wood cranesbill (*Geranium sylvaticum* L.) were most common. On good sites meadowsweet and water avens (*Geum rivale* L.) were most important. On rich sites tall-growing forbs like meadowsweet, valerian (*Valeriana sambucifolia* L.), giant bellflower and lesser celandine (*Ranunculus ficaria* L.) were fed on. On meadows meadowsweet and clover (*Trifolium* spp. L.) dominated in the diet and in grain-fields weeds like creeping buttercup (*Ranunculus repens* L.), common hemp nettle (*Galeopsis tetrahit* L.), dandelion and red clover were eaten most. The average number of bites within square plots increased from poor to rich sites: 33.7 ($n = 40$, $SE = 13.1$) on poor sites, 34,4 ($n = 63$, $SE = 7.3$) on medium sites, 44.9 ($n = 52$, $SE = 8.2$) on good sites and 58.1 ($n = 31$, $SE = 13.1$) on rich sites. However, the difference was not significant ($p>0.05$).

Roe deer use of forest habitats increased with increasing site quality. The animals also showed a preference for plantations within all site classes; the most preferred habitat was plantations on rich sites. Meadows, particularly moist sites with an abundance of meadowsweet and other forbs, were preferred throughout the summer, but utilization decreased in late summer. Grain fields were avoided (Fig. 2). There was no difference between males and females in overall habitat preference (Wilcoxon; $p>0.05$).

The comparison of vegetation on squares

Table 1. Roe deer preference for the plant species listed in Fig. 1.

Species	Preference[1]	Occurrence[2]	Significance[3]
Campanula latifolia	7.0	7	<0.05
Chamaenerion augustifolium	4.4	15	<0.05
Ranunculus ficaria	4.0	5	N.s.
Taraxacum cordatum	2.9	20	N.s.
Caltha palustris	2.7	11	<0.05
Trifolium pratense	2.2	15	<0.05
Melampyrum spp.	1.8	25	N.s.
Geranium sylvaticum	1.7	37	N.s.
Geum rivale	1.5	26	N.s.
Filipendula ulmaria	1.4	56	N.s.
Valeriana sambucifolia	1.4	30	N.s.
Ranunculus repens	1.2	55	N.s.
Trifolium repens	0.9	12	<0.05
Galeopsis spp.	0.3	38	N.s.
Anemone nemorosa	0.1	53	N.s.

[1] Average preference (number of bites/percent horizontal coverage of plant species) per sample plot.
[2] Number of sample plots where the species occurred.
[3] Indicates whether preferences for a species is significantly higher than for the species listed below, N.s. = not significant, $p>0.05$ (Kruskal-Wallis test).

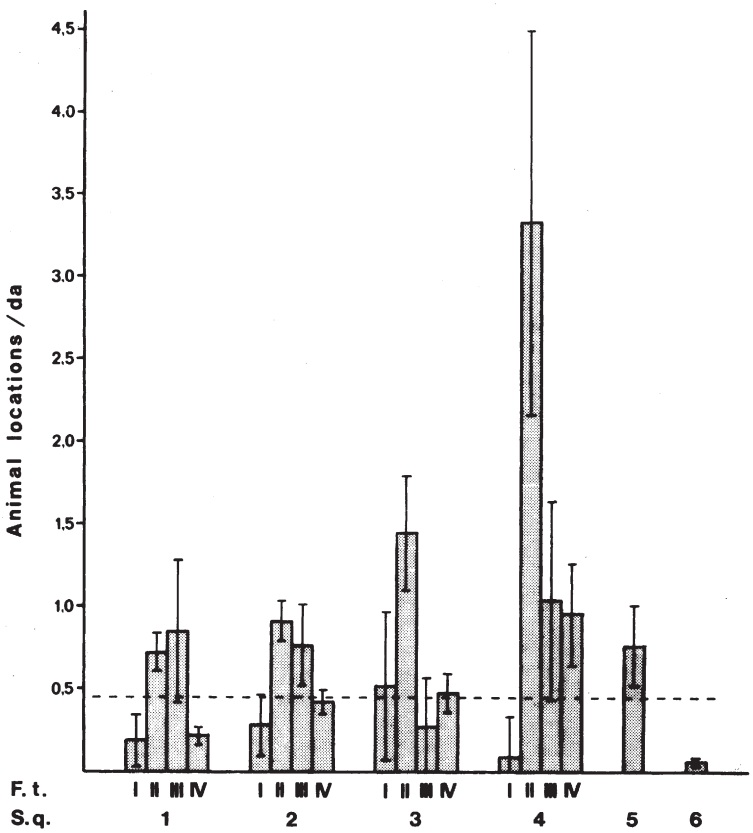

Fig. 2. Roe deer utilization of habitats within home ranges at Ås. Utilization is given as number of animal locations per da. Confidence interval is calculated according to the method of Neu et al. (1974). Broken line indicates average number of plots per da for the entire study area.
F.t. = forest types: I) clearcuts, II) plantations, III) young forest, IV) older forest (see text).
S.q. = site quality: 1) poor, 2) medium, 3) good, 4) rich, 5) meadows, 6) grainfields (see text).

of high usage and low usage supported the home range data. Seven of the high use squares were in plantations while 9 of the low use squares were in older forest. The average number of specimens of the 24 most important forage plants was higher on high use squares (4.8) than on the low-use squares (1.1) (Wilcoxon; $p<0.05$).

Roe deer used habitats differently during day and night. Young forest was used more while clearcuts and meadows were used less during the day than in nighttime. For day and night combined there was no difference in habitat utilization between early and late summer (F-test, $P>0.05$) (Fig. 3).

The animals were active during approximately 60% of the 24-hour recordings. Activity rhythms differed between early and late summer. There were shorter spans between activity peaks and smaller amplitudes during early summer than in late summer (Fig. 4).

DISCUSSION

The large number of plant species fed on by Roe deer during summer is reported in several studies (Esser 1958, Klötzli 1965, Siuda et al. 1969, Voser-Huber and Nievergelt 1975, Gebezynska 1981, Kossak 1983). However, diet apparently also reflects habitat quality and species diversity. The studies of Cederlund et al. (1980) on Roe deer in inland coniferous forests of general poor soil fertility, showed that rosebay willowherb made up nearly 60% of forage dry weight in July.

A diet composed of a large number of plant species, many of little quantitative importance, may be an adaptation to avoid high concentrations of secondary compounds from any particular plant species (van Soest 1982). Among plants fed on by Roe deer in our area, some, like bitter sweet (*Solanum dulcamara* L.), bracken (*Pteridium aquilinum* L.), herb paris (*Paris quadrifolia* L.), John's wort (*Hypericum maculatum* L) and species of the buttercup family (*Ranunculus* spp.) are poisonous (Gessner and Orzechowski 1974).

A preference ranking of forage plants is likely to be affected both by their palatability and size. Studies of White-tailed deer (*Odocoileus virginianus*) have documented that the amount of plant tissue acquired per bite has a strong influence on intake rate and feeding efficiency (Spalinger et al. 1988). Roe deer preferred good forest sites with an abundance of tall forbs. Although the number of

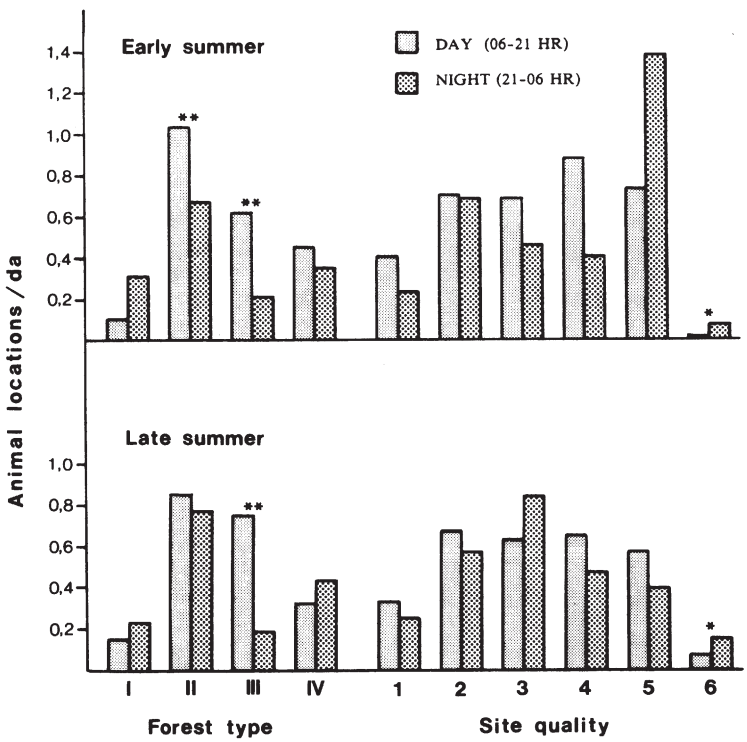

Fig. 3. Roe deer utilization of habitats within home ranges during day and night at Ås, given as number of animal locations per da. Early summer: May 1—June 30, late summer: July 1—August 31. Habitat classification as in Fig. 2.
X = Difference between day and night significant, $P<0.05$
XX = Difference between day and night significant, $P = <0.01$

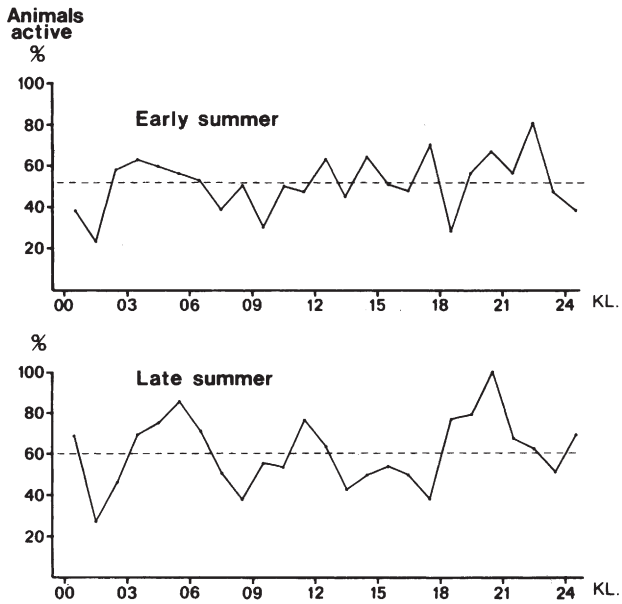

Fig. 4. Percentage of Roe bucks active over a 24-hour period during early and late summer. Broken line indicates average for the whole period. Early summer: May 1—June 30, late summer: July 1—August 31.

bites per plot did not differ significantly between poor and rich sites, the amount of forage removed per bite appeared to be much higher on large-leafed forbs growing on rich sites (giant bellflower, rosebay willowherb) compared to smaller and weaker species from poor sites like common cow-wheat.

We found increased feeding on deciduous browse and also a change in activity as the season progressed. This has also been reported in other studies (Berg 1978, Gebezynska 1980, Cederlund et al. 1980, Cederlund and Nyström 1981) and may indicate that the more fibrous forage leads to a need for longer rumination periods during late compared to early summer (Cederlund 1981, Cederlund 1989). There was also a tendency towards decreasing utilization of meadows from early to late summer, which may reflect the decreasing quality of the meadow vegetation.

The size of Roe deer populations on southern ranges appears to be regulated through social behaviour during summer, with animals holding smaller territories on good than on poor ranges (Bobek 1977). On northern ranges severe winters with deep snows cause a large die-off of animals (Borg 1958) and prevent Roe deer from occupying all potential ranges during summer. Therefore, the relative importance of winter range compared to summer range in regulating Roe deer population size will depend on latitude. In our study area, snow depth is moderate over the winter and, furthermore, Roe deer are fed extensively by local farmers. We therefore believe that the density of the Roe deer in our study area is socially regulated on their summer range and that an increase in population size is dependent on improvement of the summer habitat.

During summer, Roe deer benefit from modern forestry through the increased forage production following clear cutting. Forest plantations are also reported to be the most preferred summer habitat in several other studies (Loudon 1982, Staines and Welch 1984, Eiberle and Holenstein 1985, Lund 1986). Roe deer in our study area used open habitats like clearcuts and meadows less during the day than during the night (Fig. 3). Older plantations, on the other hand, where cover is very good but vegetation of the field layer is poor, were used extensively during daytime, both in early and late summer. This indicates that cover is an important factor in Roe deer habitat selection. From his studies in Germany, Sperber (1975) stated that forage is most abundant in spruce plantations aged 1—10 years while cover was best from 11 to 20 years of age; therefore plantations around 10 years old have the best combination of forage and cover. In our area, this would mean that later stages of plantations give Roe deer an ideal habitat.

This study has clearly demonstrated that rich sites with abundant growth of forbs and browse offer Roe deer the best summer forage. Assuming that summer range determines population size of Roe deer in this part of Norway, a reduction of the production of ground vegetation on rich sites through agricultural or forestry operations will reduce the carrying capacity of the range. Application of herbicides to reduce forbs and deciduous brush on forest plantations or the conversion of rich, moist meadows to grass or grain fields may therefore be expected to have a negative effect on Roe deer population size.

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