

Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales

Authors: Gundersen, Hege, Andreassen, Harry P., and Storaas, Torstein

Source: Wildlife Biology, 10(3) : 213-223

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2004.027>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales

Hege Gundersen, Harry P. Andreassen & Torstein Storaas

Gundersen, H., Andreassen, H.P. & Storaas, T. 2004: Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales. - Wildl. Biol. 10: 213-223.

Landowners in southeast Norway have supplied moose *Alces alces* with ensiled bales of hay for up to eight winters. The incentive has been to limit migratory movements into heavily trafficated winter areas and away from young forest plantations. In this article, we report on landscape characteristics that increase the use of feeding stations, and on how browsing activity on Scots pine *Pinus sylvestris* twigs as well as leader stems of both pine and Norway spruce *Picea abies* was associated with distance to feeding stations at two different spatial scales: 1) at a local scale we sampled data from 50 m² observational plots up to 200 m from the feeding stations, and 2) at a regional scale we sampled data at all available young forest plantations up to 7 km from a feeding station. The probability that a feeding station was used increased towards the bottom of side valleys. The frequency of use of feeding stations increased annually, with increasing distance to other feeding stations, and with increasing distance to the more populated main valley. Moose-induced browse damage was extensive at proximate distances (< 200 m) to feeding stations, decreased to a minimum at 1-2 km, and increased slightly again at 3-7 km distance from less intensely used feeding stations. Indices of moose activity distribution (i.e. piles of faecal pellets) resembled browsing activity.

Key words: forest damage, game-vehicle accidents, mitigative effort, moose management, *Picea abies*, *Pinus sylvestris*, seasonal migration, supplemental feeding

Hege Gundersen, Harry P. Andreassen & Torstein Storaas, Hedmark University College, Evenstad, N-2480 Koppang, Norway - e-mail addresses: hege.gundersen@bio.uio.no (Hege Gundersen); harry.andreassen@sue.hihm.no (Harry P. Andreassen); torstein.storaas@sue.hihm.no (Torstein Storaas)

Corresponding author: Hege Gundersen

Received 14 May 2003, accepted 13 October 2003

Associate Editor: Atle Mysterud

Ungulate populations are often characterised by migratory movements between summer and winter ranges (Sinclair 1983), and both vehicle accidents and forest damage are connected to peaks on migration periods (for moose *Alces alces* migration see LeResche 1974, Pulliainen 1974, Hundertmark 1998). Such seasonal movements by moose may be fairly long, crossing arteries with

heavy traffic and involve high risk of moose-vehicle accidents (Andersen, Wiseth, Pedersen & Jaren 1991, Gundersen, Andreassen & Storaas 1998). Further, high densities of moose concentrated in winter ranges close to young forest stands often lead to severe forest damage (Lavsund 1987, Lääperi 1990, Danell, Niemela, Varvikko & Vuorisalo 1991, Heikkilä & Härkönen 2000)

with high costs for the landowners (Storaas, Gundersen, Henriksen & Andreassen 2001). Today, the amount of damage to young pine stands in Scandinavia often sets the practical limits for the moose density in areas with intensive forestry (Lavsund 1987), whereas little effort has been made to deal with this problem in a way that does not involve a reduction of the moose population (but see Ahlén 1975).

For cervids in the northern hemisphere, winter ranges are typically located at lower elevations or within areas having less severe snow conditions than ranges utilised at other times of the year (Cederlund, Sandegren & Larsson 1987). Migration is often initiated by seasonal cues such as high precipitation and snow cover (Marchinton & Hirth 1984, Cederlund et al. 1987, Andersen et al. 1991, Nicholson, Bowyer & Kie 1997, Gundersen et al. 1998, Hundertmark 1998, Irwin 2002, Sabine, Morrison, Whitlaw, Ballard, Forbes & Bowman 2002). Thus, migrations may fail to take place in years of little snowfall (Houston 1968, Van Ballenberghe 1977, Andersen et al. 1991, Ballard, Whitman & Reed 1991). Migration routes and winter ranges seem to be bound by tradition, as calves follow their mothers to their winter ranges, and in subsequent years establish their own winter ranges close to the maternal range (Baker 1978, Cederlund et al. 1987, Sweanor & Sandegren 1989, Andersen 1991). Therefore, it seems difficult to change moose migratory behaviour to avoid human conflicts without establishing strong barriers such as fences.

Migrations have mainly been viewed as an adaptation to optimise food resources (Baker 1978, but see Sinclair 1983). If the migration to winter ranges is a snow-induced movement performed to increase food resources, we may assume that supplementation of food along migration routes will actuate one or more of the following scenarios: 1) decrease the number of migratory individuals (as found among winter fed white-tailed deer *Odocoileus virginianus*; Lewis & Rongstad 1998), 2) decrease the distance of migration, or 3) delay migration so that fewer moose will be located in confined areas and for a shorter period of time. Experimental studies have shown that mammalian behaviour may be altered by supplemental feeding (see Boutin 1990 for a review). Small mammals may aggregate around feeding stations and shrink their home ranges (Ims 1987, Boutin 1990). Cervids also reduce their ranges when supplementary fed, as shown by Guillet, Bergström & Cederlund (1996) in studies of roe deer *Capreolus capreolus* and Schmidt (1993) in studies of alpine red deer *Cervus elaphus hippelaphus*, or move their core areas closer to bait (white-tailed deer; Kilpatrick & Stober 2002). Wood & Wolfe (1988) showed that intercept feeding

reduced the number of mule deer *Odocoileus hemionus* collisions along highways in Utah, USA. If the response to supplemental feeding is the same for other ungulates, this technique could be applied to manipulate the distribution of big game animals away from troublesome areas such as highways, industrial forests and cultivated fields (see Smith 2001).

Several cervids are fed by humans to increase winter survival and thus maintain artificially high winter densities (Boyce 1989). Other rationales to feed may be to reduce crop and forest damage, for commercial reasons such as game viewing, and for management purposes such as trapping and disease control (see Schwartz & Hundertmark 1993, Heikkilä & Härkönen 2000, Smith 2001, Peek, Schmidt, Dorrance & Smith 2002). Lately, other aspects of supplemental feeding, both positive and negative (see Smith 2001), have emerged, in particular, the spatial distribution of browsing activity and forest damage around feeding stations (Doenier, DelGuidice & Riggs 1997). Knowledge on the effects of feeding has mainly emerged from the literature on elk/red deer (e.g. Boyce 1989), and little is known about the effects of supplemental feeding on moose-human conflicts (but see Lääperi 1990). This study is based on a moose winter feeding programme that was initiated and financed by landowners in southeast Norway in the beginning of the 1990s. The supplemental feeding was carried out in an area with a high number of moose-vehicle accidents (Gundersen et al. 1998), because it was expected to reduce migration of moose and hence the number of vehicle accidents. We studied how supplemental winter feeding correlates with the spatial distribution of browsing activity at a local scale surrounding the feeding stations. At a regional scale, we studied how browsing of young forest plantations was connected to the distance to feeding stations. Furthermore, we also searched for landscape and habitat factors associated with a frequent utilisation of feeding stations by moose.

Material and methods

Study area

The study area is located in the municipality of Stor-Elvdal in the county of Hedmark, southeast Norway (~61°N, 11°E; Fig. 1). The vegetation is dominated by pure or mixed stands of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Interspersed are small amounts of boreal deciduous species such as birch *Betula pubescens*, willow *Salix* spp., mountain ash *Sorbus aucuparia*, aspen *Populus tremula* and hoary alder *Alnus incana*. The Glomma River runs along Østerdalen, a main val-

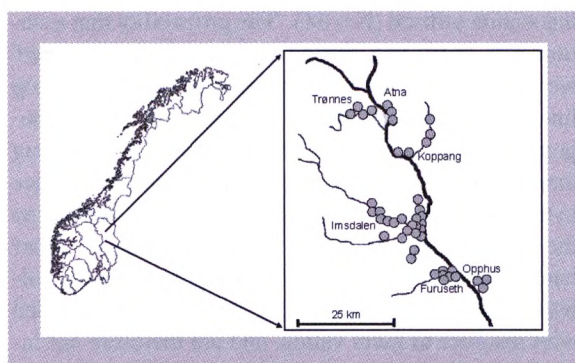


Figure 1. Location of the 44 moose feeding stations (●) and the six feeding areas in our study area situated in the municipality of Stor-Elvdal. Thick lines indicate the main valley, Østerdalen and Glomma River, and the thin lines indicate the side valleys.

ley of southeastern Norway. In our study area, Glomma is about 250–350 m a.s.l. and is surrounded by forested hills and mountains (400–1,100 m a.s.l.). At Evenstad weather station, 20 km south of Koppang (see Fig. 1), at 250 m a.s.l. the mean winter (1 November – 31 March) temperature for the last 30 years is -6.4°C ($\text{SD} = 7.1$) and mean snow cover for the same period is 39.9 cm ($\text{SD} = 30.7$). Climatic values from the winter when registrations were performed for the present study (1997/98) were -4.3°C ($\text{SD} = 5.5$) and 32.1 cm ($\text{SD} = 15.5$) for temperature and snow cover, respectively. Data on mean depth of snow cover in the surrounding mountains are not available, but it is somewhat deeper than in the valleys.

From hunter observations (Solberg & Sæther 1999) we know that during the hunting season in September–October, most moose are located at higher elevations, in areas with generally high precipitation. When snow accumulates in the summer areas, moose move to areas characterised by lower precipitation, and when snow depth further increases, they concentrate along the Glomma River in the main valley (Gundersen et al. 1998). Experience from landowners and a radio-tracking study (Odden, Linnell, Støen, Gangås, Ness & An-

dersen 1996) suggest that the main migratory routes follow the side valleys of Østerdalen valley (see Fig. 1).

The cervid community in our study area is dominated by moose (~ 1.1 moose/ km^2). However, there is a sparse roe deer population in the area, and red deer have recently colonised the area, but are still occurring in very small numbers only.

Supplemental feeding

Supplemental winter feeding of moose was initiated by landowners at six different feeding areas within the Stor-Elvdal municipality (see Fig. 1), with a total of 44 feeding stations during the winter of 1997/98 (see Table 1 for variation in feeding practice between areas). The various stations were established during a period of eight years, the first during the winter of 1990/91.

The supplemental food consisted of baled and silaged graminoids and/or herbs of varying breed and combinations, usually oat *Avena sativa* and rape *Brassica napus*. One bale of silage weighed about 600 kg. Feeding stations were located in forest areas at the bottom, along hillsides, or at the outlets of the side valleys assumed to be used by moose during migration (Odden et al. 1996). All stations were placed near snow free roads with low human activity, so that the food could easily be supplied by car. Additional food supplementation was performed when the previously supplied food was eaten. The feeding period covered 5–6 months. Snow accumulation in the hillsides, usually in December, indicated the starting time of the feeding period, and the time of snow melt or initiation of summer migration in April–May set the end point.

Field procedures

During the summer of 1998 (20 May – 31 July) we registered the browsing activity from the previous winter (1997/98) on 50- m^2 circular plots located at 1) a local scale (within 200 m from the feeding stations) and 2) a regional scale (up to 7 km from feeding stations). At the local scale, we placed the plots at 12.5 m, 25 m, 50

Table 1. Values of various feeding practices in the six feeding areas. 'Feeding stations' are presented as used number of feeding stations / total number of feeding stations available. 'Forest stands' show the number of young forest stands surveyed. 'Years' give the mean (range) number of years the feeding stations have been operated. 'Bales' give the mean (\pm SD) number of bales utilised per feeding station the year of survey. The distances are presented with the mean (\pm SD) for all feeding stations in each area. The feeding areas at Atna and Opphus are not located by side-valleys, and we have thus used distance to the main valley as the descriptor both of main valley and side valley.

Feeding area	Feeding stations	Forest stands	Years	Bales	Distance (km) to the nearest		
					Feeding station	Main valley	Side valley
Atna	2 / 3	7	6.0 (6, 6)	8.7 ± 6.7	2.8 ± 0.2	0.9 ± 0.2	0.9 ± 0.2
Furuseth	3 / 7	7	2.0 (2, 2)	1.7 ± 1.1	0.3 ± 0.1	1.0 ± 0.5	0.8 ± 0.4
Imsdalen	18 / 22	28	5.1 (1, 8)	5.3 ± 3.8	1.2 ± 0.8	3.8 ± 3.4	0.8 ± 1.1
Koppang	5 / 5	8	4.0 (4, 4)	13.0 ± 7.2	2.5 ± 1.3	3.6 ± 3.0	0.6 ± 0.6
Opphus	0 / 3	0	3.0 (3, 3)	1.0 ± 0.0	0.5 ± 0.5	1.0 ± 0.7	1.0 ± 0.7
Trønnes	3 / 4	8	2.5 (1, 3)	20.3 ± 17.4	2.0 ± 0.5	4.5 ± 1.9	0.8 ± 0.5

m, 100 m and 200 m from each feeding station. For each distance we selected four plots, located north, south, east and west, respectively, yielding 20 plots around each feeding station. Inaccessible plots in rivers and ponds were excluded. At 13 feeding stations that showed few or no signs of moose activity (e.g. lack of faecal pellets and remaining silaged hay), we surveyed only at the four plots situated 12.5 m from the feeding station. At the regional scale we selected all young forest stands available ($N = 63$) within a maximum distance of 7 km from a feeding station. At each young forest stand four plots, located randomly with at least 20 m spacing, and at least 20 m from the edge of the stand, were surveyed.

The preceding year's winter browsing was easily separated from earlier years' browsing by colour and moisture of the cut edge of the twigs. On each plot we registered browsing activity on all trees between 0.5 and 3 m, which is approximately the height accessible for moose during winter, snow cover taken into consideration. On pine, we counted the number of leader stems and the number of lateral twigs browsed upon, and the total number of leader stems and lateral twigs available during the previous winter. On spruce, we registered only browsing of leader stems because lateral twigs of spruce are seldom browsed by moose (Bergström & Hjeljord 1987 and references therein). On deciduous trees we counted the number of twigs available and browsed upon last winter. A total of 260,000 twigs on 11,000 trees were counted.

To get a more direct descriptor of moose activity distribution we also counted the number of piles of faecal pellets in each plot.

Data analyses

Correlates to utilisation intensity

To explore how utilisation intensity of feeding stations was associated with the surroundings, we defined two responses: 1) whether the feeding station had been used by moose at all (i.e. the probability of use), and 2) the number of bales of silage consumed at each feed-

ing station utilised ($N = 31$). 'The probability that a station was used' and 'the number of bales consumed' were analysed in a logistic (binomial error) and a log linear (poisson error) model, respectively. From topographic maps (1:50,000) we included the following three landscape variables as predictors: altitude, distance to the bottom of the nearest side valley, and distance to the bottom of the main valley (i.e. Østerdalen). Other landscape features such as distance to main roads, railways and human settlements are completely confounded with distance to main valley, and are therefore not included in the analyses. In addition we included a predictor of feeding practice: distance to the nearest used neighbouring feeding station. The distance predictors were log-transformed in the model to avoid disproportionate influence from outlying observations.

The distance variables mentioned above are well suited to describe the landscape because all distance variables span several kilometres, but give no insight into characteristics of the immediate surroundings of frequently used feeding stations (Table 2). Hence, to see if local habitat characteristics had an effect on the utilisation of feeding stations we also included total number of available twigs (irrespective of tree species) as a predictor of habitat quality in the models, i.e. in the analyses of the probability of use we used the mean of all available twigs from the four plots at 12.5 m distance (as the other distances were not surveyed at feeding stations that had not been used). In the analyses of number of bales consumed we entered both the mean of all available twigs from the four plots at 12.5 metres' distance and the mean of all available twigs for all plots surrounding the feeding station (i.e. up to 200 m radius).

All analyses were performed by a backwards selection procedure excluding non-significant ($P > 0.05$) terms from the model.

We also performed a poisson regression analysis to see how duration of feeding (number of years) correlated with the number of bales consumed at the feeding stations located in Imsdalen. We only used the

Table 2. Description of predictors used in the full models of 'the probability of utilisation' and 'the number of bales consumed'. Mean available twigs up to 200 m was not included in the analyses of the probability of utilisation as we only registered plots at 12.5 m for feeding station that had not been used. Range is given with minimum and maximum values.

Predictor	Description	Range
Distance to nearest side valley	Distance (in km) from the feeding station to the bottom of the valley.	0.05 - 4.9 (km)
Distance to main valley	Distance (in km) from the feeding station to the Glomma River at the bottom of the main valley (Østerdalen).	0.2 - 4.9 (km)
Distance to nearest used feeding station	Distance (in km) to the nearest used feeding station.	0.25 - 4.4 (km)
Altitude	Metres a.s.l.	255 - 760 (m)
Mean available twigs at 12.5 m	Mean of all twigs available (irrespective of tree species) from the maximum of four plots sampled at 12.5 m from the feeding station.	0 - 1397
Mean available twigs up to 200 m	Mean of all twigs available (irrespective of tree species) from the maximum of 20 plots sampled up to 200 m from the feeding station.	0.7 - 904

Imsdalen area because in this area moose supplementary feeding has been carried out for most years, and it is the only area with some variation in duration of feeding between stations (i.e. 1-8 years; see Table 1). Even though there is some variation also in the Trønnes area, supplementary feeding has just recently been initiated in this area (maximum of three years).

Forest damage

We performed the analyses of forest damage at the level of plot, using feeding station and feeding area as random factors. In the analyses at the regional scale, we also included young forest stand as a random factor. The statistical modelling was performed in the SAS-macro GLIMMIX that estimates an F-ratio as the test statistic (Littell, Milliken, Stroup & Wolfinger 1996). The random factors were introduced to the model in a hierarchical structure to control for potential dependencies at the level of feeding station and area.

We analysed two indices of browse activity by developing logistic random models: 1) the proportion of the available lateral twigs of pine browsed in each plot, and 2) the proportion of leader stems of pine and spruce browsed in each plot. The main factor applied as a fixed predictor in the models was the distance (DIST) from the observational plot to the nearest utilised feeding station (stations not used by moose were excluded). In addition we included the number of silage bales (BALES) consumed at each station as a cofactor. In the analyses of the proportion of leader stems browsed we also included the variable tree species (TREE, i.e. pine and spruce). We included all two-way interactions in the full model, and the squared variables DIST*DIST and BALES*BALES. The squared variables were included to explore possible non-linear relations. The modelling was done by excluding non-significant ($P > 0.05$) terms in a backward selection procedure. The distance to the nearest feeding station and the number of bales consumed were log-transformed in the analyses to avoid disproportionate influence from outlying obser-

vations. Hence, the full logistic models applied to analyse browse activity at the plot level were as follows:

- 1) Lateral twigs browsed/available = DIST + BALES + DIST*BALES + DIST*DIST + BALES*BALES
- 2) Leader stems browsed/available = DIST + BALES + TREE + DIST*BALES + DIST*TREE + BALES*TREE + DIST*DIST + BALES*BALES

Moose distribution

To confirm that moose activity distribution pattern resembled browsing activity, we analysed the number of piles of faecal pellets, applying a log-linear model including the variables 'DIST' and 'BALES' and all two-way interactions. The analyses were performed at the plot level with region and feeding station as random factors.

Results

Utilisation of feeding stations

The probability that a feeding station had been used during winter decreased with increasing distance to the bottom of the side valley (Table 3). The number of bales consumed at the feeding stations used increased with increasing distance to the main valley and with increasing distance to the nearest neighbouring feeding station (see Table 3). Descriptors of local habitat quality (availability of twigs) were not selected in the statistical models (all $P > 0.175$).

At the Imsdalen feeding area, the number of bales consumed increased with the number of years the feeding station had been used (logit slope (\pm SE) = 0.11 (\pm 0.05); $F_{1,16} = 5.06$, $P = 0.025$).

Forest damage

Within the local scale (< 200 metres) the proportion of lateral pine twigs browsed decreased with increasing dis-

Table 3. Statistical models for the probability that a feeding station had been used and the number of bales consumed per feeding station. The estimates are given for the logistic model with binary error: Logit (probability of use) = predictors and the log linear model with poisson error: Log (number of bales) = predictors. All distance predictors are log-transformed in the model and are defined as the shortest distance from the feeding station to a side valley, a main valley or another feeding station. The F-ratio is presented with nominator (NDF; i.e. model) and denominator (DDF; i.e. error) degrees of freedom. A total of 44 feeding stations were sampled, but only the 31 stations used were introduced into the model describing the number of bales consumed.

Response	Predictors	Estimate \pm SE	$F_{NDF,DDF}$	P
Probability of use	Intercept	0.28 \pm 0.58		
	Distance to side valley	-1.10 \pm 0.49	4.83 _{1,42}	0.034
Number of bales	Intercept	1.96 \pm 0.08		
	Distance to main valley	0.18 \pm 0.05	10.88 _{1,28}	0.001
	Distance to neighbouring feeding station	0.52 \pm 0.09	37.88 _{1,28}	< 0.001

Table 4. Statistical models of the proportion of lateral pine twigs browsed at a local and a regional scale. The estimates are given for the logistic model with binary error: Logit (proportion of lateral pine twigs browsed) = predictors. Distance and number of bales consumed (Bales) are log-transformed in the model. Distance at a local scale has a maximum value of 200 m from the feeding station, whereas at the regional scale data stem from observations at young pine stands up to 7 km from the feeding stations. Region and feeding station were used as random factors in the models. The F-ratio is presented with nominator (NDF; i.e. model) and denominator (DDF; i.e. error) degrees of freedom.

Spatial scale	Predictors	Estimate \pm SE	F _{NDF,DDF}	P
Local	Intercept	-6.59 \pm 2.28		
	Distance	3.20 \pm 1.11	8.26 _{1,333}	0.004
	Bales	1.53 \pm 0.41	14.09 _{1,333}	< 0.001
	Distance*Bales	-0.53 \pm 0.14	14.85 _{1,333}	< 0.001
Regional	Intercept	-3.16 \pm 1.07		
	Distance	1.27 \pm 0.96	1.74 _{1,80}	0.191
	Bales	0.34 \pm 0.49	0.47 _{1,80}	0.494
	Distance*Distance	0.75 \pm 0.32	5.40 _{1,80}	0.023
	Distance*Bales	-1.06 \pm 0.50	4.44 _{1,80}	0.038

tance to the feeding station, in addition to a positive correlation with the number of bales consumed (Table 4, Fig. 2A). Hence, a higher proportion of pine twigs were browsed in the vicinity of intensely used feeding stations.

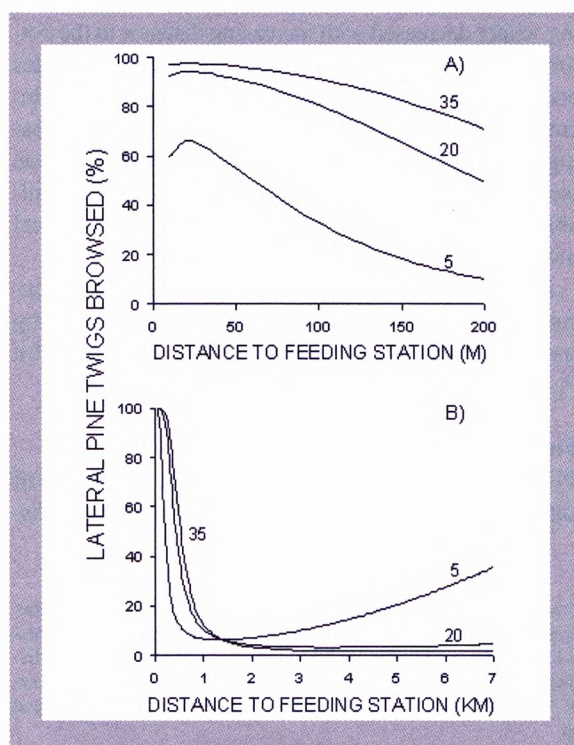


Figure 2. Proportion of available pine twigs browsed relative to distance to feeding station and number of bales (marked on the predicted lines) of silage consumed at the local (A) and regional (B) scale. The figures above the curves (5, 20 and 35) represent the number of bales that were chosen to visualise the interaction between the two variables. For standard errors of the estimates see Table 4.

Table 5. Statistical models of the proportion of leader stems browsed at a local and a regional scale. The estimates are given for the logistic model: Logit (proportion of leader stems browsed) = predictors. Distance is log-transformed in the model. The F-ratio is presented with nominator (NDF; i.e. model) and denominator (DDF; i.e. error) degrees of freedom. Region and feeding station were entered into the models as random factors.

Spatial scale	Predictors	Estimate \pm SE	F _{NDF,DDF}	P
Local	Intercept	-4.71 \pm 1.95		
	Distance	2.44 \pm 1.13	6.66 _{1,512}	0.01
	Species		5.15 _{1,37}	0.029
	Pine	-2.53 \pm 1.11		
	Spruce	0.00		
	Distance*Distance	-0.56 \pm 0.16	11.52 _{1,512}	0.001
	Species*Distance			
Regional	Pine	1.21 \pm 0.32	13.81 _{1,512}	< 0.001
	Spruce	0.00		
	Intercept	-3.55 \pm 0.40		
	Distance	-0.10 \pm 0.20	0.27 _{1,201}	0.604
	Species		25.73 _{1,29}	< 0.001
	Pine	1.82 \pm 0.36		
	Spruce	0.00		
	Distance*Distance	0.40 \pm 0.17	5.81 _{1,201}	0.017

At the regional scale, pine twig browsing decreased abruptly up to about 1 km from the feeding station (see Table 4, Fig. 2B). However, an interaction between distance and the number of bales consumed showed an increase in twig browsing at about 3-7 km from less

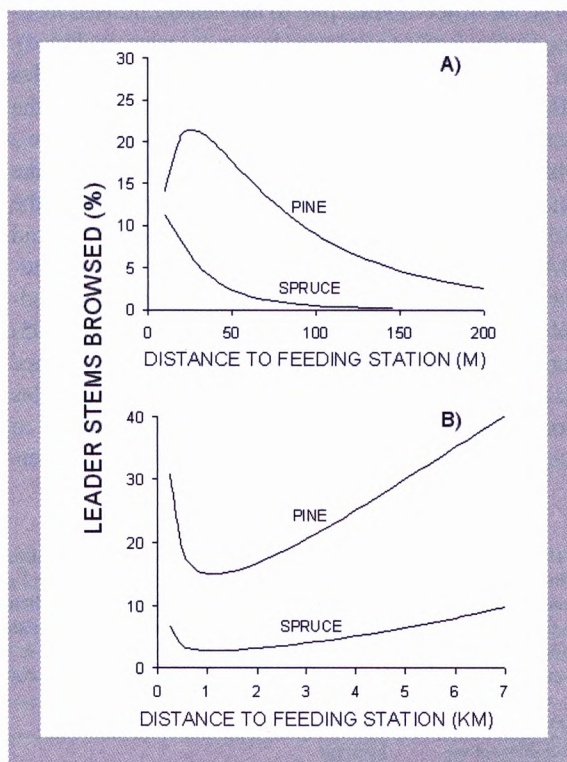


Figure 3. Browsed leader stems of pine and spruce relative to distance to feeding station at the local (A) and regional (B) scale. For standard errors of the estimates see Table 5.

Table 6. Statistical models of the number of piles of faecal pellets at a local and regional scale. The estimates are given with poisson error: $\text{Log}(\text{number of piles}) = \text{predictors}$. Region and feeding station were entered into the models as random factors. The F-ratio is presented with nominator (NDF; i.e. model) and denominator (DDF; i.e. error) degrees of freedom. Variation in the DDF is due to missing values, i.e. plots lacking the tree species in question.

Spatial scale	Estimate \pm SE	F _{NDF,DDF}	P
Local			
Intercept	-3.75 \pm 0.89		
Distance	3.26 \pm 0.48	45.64 _{1,576}	< 0.001
Bales	0.65 \pm 0.16	16.93 _{1,576}	< 0.001
Distance*Distance	-0.56 \pm 0.07	66.39 _{1,576}	< 0.001
Regional			
Intercept	-2.24 \pm 0.47		
Distance	-0.56 \pm 0.21	7.33 _{1,172}	0.008
Bales	0.81 \pm 0.22	13.33 _{1,172}	< 0.001

intensely used feeding stations. At feeding stations with high consumption of bales, browsing was generally low at distances more than 1 km from the feeding station.

The proportion of pine leader stems browsed was higher than that of spruce leader stems (Table 5, Fig. 3). For both pine and spruce, the influence of distance to feed-

ing stations on the proportion of leader stems browsed had a pattern similar to lateral pine twigs browsed, both at the local (Fig. 3A) and the regional (Fig. 3B) scale. Compared to the models selected for the analyses of lateral twigs, however, there was no correlation between leader stems browsed and bales consumed.

Moose distribution

Similar to browsing damage, the number of faecal pellets was associated with distance to feeding station and the number of bales consumed both at the local and the regional scale (Table 6, Fig. 4).

Discussion

The high density of moose in Scandinavia contributes to increased moose-human conflicts. Supplemental feeding may be one way to mitigate these conflicts, but the association between feeding and the release of human conflicts is generally poorly reported. Traditionally, supplemental feeding of cervids has been performed primarily as an emergency effort to enhance survivorship of populations experiencing harsh climatic conditions during winter (see Smith 2001 for other rationales of feeding). Populations of elk (Boyce 1989), *Odocoileus* spp. (Ozoga & Verme 1982, Baker & Hobbs 1985, Ouellet, Crête, Maltais, Pelletier & Huot 2001), roe deer (Cederlund 1982), and reindeer *Rangifer tarandus* (Aagnes & Mathiesen 1995) are often dependent on additional feed to maintain high densities during severe winters. Supplemental feeding of moose during winter has been tested both as emergency feeding (Schwartz & Hundertmark 1993) and with the intention of reducing forest damage (Lääperi 1990, Heikkilä & Härkönen 2000). These studies show that moose utilise feeding of various kind such as hay, forest residues and mineral licks. It has, however, not been reported how forest damage is associated with winter feeding of moose.

The number of bales consumed show that moose utilise supplemental feeding during winter. Further, the association found between the amount of faecal pellets and distance to feeding station show that the general moose activity distribution is concentrated around feeding stations, either because some moose spend more time close to feeding stations or because more moose aggregate around feeding stations. However, our study suffers from complications common to observational studies. For instance, the feeding stations were not randomly located, but placed where the landowners expected them to be used. In spite of this, however, moose apparently need to learn the location of feeding

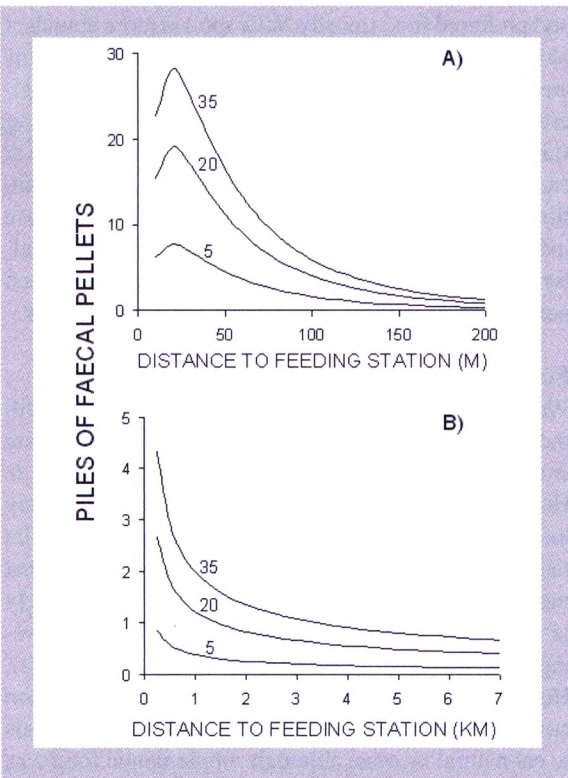


Figure 4. Number of piles of faecal pellets relative to distance to feeding station and number of bales (marked on the predicted lines) of silage consumed at the local (A) and regional (B) scale. The figures above the curves (5, 20 and 35) represent the number of bales that were chosen to visualise the interaction between the two variables. For standard errors of the estimates see Table 6.

sites (Bailey, Gross, Laca, Rittenhouse, Coughenour, Swift & Sims 1996), and maybe also to eat silage. At Opphus (see Fig. 1), the moose were offered silage for four years before they started to feed on it (S. Myrbakken, pers. comm.). In Imsdalen, the use of feeding stations increased over the years. These results indicate that moose remembered the location of the feeding station and returned to it, or that more moose through time found the feeding station and hence, the number of moose at each station increased. Thus, even though feeding stations were placed so as to optimise their use according to landowner experience, their location may have been wrong at the time of first application. Our observations may be further justified based on the following arguments: 1) at a local scale optimising the location of feeding stations was limited by the presence of roads cleared of snow; 2) if the deliberate location of feeding stations somewhat affected our results, the expected browsing intensity should then decrease steadily with increasing distance to the feeding station, not increase again at far distances from the feeding sites (5–7 km); and 3) the large scale of the study comprising various feeding areas with variable landscape parameters, feeding practice and success of feeding (i.e. probability of use and number of bales used) do break apart some of the confounding between feeding sites and environmental variables. In addition, if feeding is supposed to be an option for management, it must also be applicable (e.g. close to roads), and for those managing their lands the robustness of our results is somehow increased compared to an artificial study design with less basis in reality for management.

Our study also suffers from having had only one year of data sampling. Thus possible temporal differences due to for instance variable winter severity are not revealed (Doenier et al. 1997). However, when we compare climatic values for the year of study with average values from the last 30 years, the year of data sampling lies well within the standard deviations of both temperature and snow depths (see Material and methods). Thus, our results on forest damage and utilisation distribution regarding supplemental feeding can be considered within the confined borders of a 'normal' winter.

Utilisation of feeding stations

Feeding stations located in or near the bottom of side valleys used during moose migration (Odden et al. 1996) had a higher probability of being used than feeding stations farther away. In addition, feeding stations were more intensely used far from the main valley, Østerdalen, and far from neighbouring feeding sta-

tions. But we found no association between utilisation of feeding stations and available browse used as a descriptor of local habitat quality. Utilisation of feeding stations therefore seems to be determined by large-scale landscape patterns and not by the habitat surrounding the feeding stations. This may indicate that feeding stations intercept migrating moose, and to a lesser extent the residential segment of the population that have their home range in the feeding areas. The reason for this is that we expect the activity distribution of resident moose to depend more on local habitat quality, and to a lesser extent on large-scale landscape parameters.

We have no data on movement of moose or how individual moose used the feeding stations. The following interpretation of these results can thus be no more than speculative, but it may nevertheless give rise to the following hypotheses for future studies: 1) the greatest number of moose is intercepted at an early point of the migration, resulting in fewer individuals remaining for subsequent stations; 2) moose migration route, when it proceeds after the outlet of a side valley, is unpredictable from landscape features, and thus difficult to intercept with feeding stations; 3) availability of alternative and preferred food (mostly *Salix* spp.) is more abundant along the main valley, hence less silage is eaten in this area; and 4) the number of consumed bales of silage increased with increasing distance to another feeding station which may indicate that the feeding pressure at each station is best relieved by placing neighbouring stations close to each other. Whether different moose individuals are faithful to 'their' feeding station, or alternatively, the same individuals alternate between neighbouring stations, is a subject for future studies.

Forest damage

We found that winter moose feeding inevitably will induce a high degree of browsing in the immediate surroundings of the feeding station. Schwartz & Hundertmark (1993) found that moose that fed on hay lost weight compared to moose feeding on a pellet ration. Hence, browsing activity may reflect the fact that moose need other food items in addition to the supply of silage, and therefore will use other food while browsing near the feeding stations (Doenier et al. 1997). However, Schmitz (1990) concluded that competition among white-tailed deer at feeders forced individuals to eat natural browse, although supplemental food was provided *ad libitum*. Intensified conflicts and social strifes (Bubenik 1998) have been demonstrated among white-tailed deer (Ozoga 1972) and red deer (Veiberg, Loe, Mysterud, Langvatn & Stenseth 2004) sharing a confined feeding area during winter, and have also been

shown among moose at mineral licks during summer (Couturier & Barrette 1988). Such intra-specific interactions have also been observed in our study area (T. Storaas, unpubl. data). The amount of browsing damage around heavily used feeding stations in our study area could therefore also be due to competition between individuals.

It appears that moose feeding will cause forest damage close to intensively used feeding stations and probably up to 1 km from the station. Forest damage is, however, limited at distances farther away than 1 km, particularly around intensively used feeding stations. Contrary to our results, Doenier et al. (1997) found an increasing degree of browsing with increasing distances (up to 900 m) to white-tailed deer feeders and proposed that a greater proportion of preferred browse species were present at increasing distances from feeders. Additional comparative studies are needed to point out whether this is attributed to differences between species or habitat characteristics.

Management implications

Manipulating the moose distribution by supplemental feeding is probably most successful if the stations are placed at an early point of the migration routes and as close to the route as possible. Further, we recommend that new feeding stations should be established more than 1 km from vulnerable young forest stands and traffic arteries, but one cannot assume any reduction in browse damage at distances beyond 5-7 km from the feeding station.

However, feeding of cervids during winters is questionable as summarised by Smith (2001). The aggregation of animals makes them more susceptible for the spread of diseases (Smith 2001), and the alteration of plant communities due to dense moose population may alter the whole ecological community (Berger, Stacey, Bellis & Johnson 2001). If the moose population increases due to enhanced survival or fecundity, feeding stations may induce more moose to browse away from feeding grounds due to agonistic behaviour (Schmitz 1990). As our results show, the number of consumed bales increased with increasing distance to another feeding station, which may suggest a higher number of moose at isolated feeding stations. Hence, intra-specific interactions may be relieved by distributing a higher number of feeding stations.

Conclusion

If moose migration to winter ranges is an adaptation to optimise food availability (Baker 1978, but see Sinclair

1983) there is good reason to believe that providing additional food supplies along the migration route will affect moose migratory behaviour and probably also their spatial distribution during winter. Assuming that heavy browsing activity is correlated with moose density, here shown by the correlation with faecal pellets, our results suggest that moose aggregate around feeding stations. Hence, in accordance with studies on other mammals (Wood & Wolfe 1988, but see Boutin 1990), feeding stations seem to affect also the distribution of moose during winter. The results of our study suggest that feeding stations that have been used for several years may help reducing damage on young forest plantations up to 5 km from the feeding station, on the expense of heavy destruction of forest in the close vicinity to feeding stations.

To increase our understanding of the effects of winter feeding, future studies should concentrate on unravelling the number of moose and which individuals are actually using each feeding station, how long time they spend at a feeding station, and the intra-specific interactions between various categories of animals at feeding stations.

Acknowledgements - we thank employees and students at Hedmark University College, Evenstad, for technical assistance and fieldwork and local landowners for being co-operative and helpful. We also thank R.A. Ims for valuable comments on the manuscript. The State Bank of Agriculture, Glommen forest owner union and Hedmark University College supported the project financially.

References

- Aagnes, T.H. & Mathiesen, S.D. 1995: Round baled grass silage as food for reindeer in winter. - *Rangifer* 15: 27-35.
- Ahlén, I. 1975: Winter habitats of moose and deer in relation to land use in Scandinavia. - *Viltrevy* 9: 45-192.
- Andersen, R. 1991: Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. - *Journal of Applied Ecology* 28: 102-108.
- Andersen, R., Wiseth, B., Pedersen, P.H. & Jaren, V. 1991: Moose-train collisions: Effects of environmental conditions. - *Alces* 27: 79-84.
- Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. 1996: Mechanisms that result in large herbivore grazing distribution patterns. - *Journal of Range Management* 49: 386-400.
- Baker, D.L. & Hobbs, N.T. 1985: Emergency feeding of mule deer during winter: tests of a supplemental ration. - *Journal of Wildlife Management* 49: 934-942.

- Baker, R.R. 1978: The evolutionary ecology of animal migration. - Holmes and Meier, New York, 1012 pp.
- Ballard, W.B., Whitman, J.S. & Reed, D.J. 1991: Population dynamics of moose in south-central Alaska. - *Wildlife Monographs* 114, 1-49 pp.
- Berger, J., Stacey, P.B., Bellis, L. & Johnson, M.P. 2001: A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. - *Ecological Applications* 11: 947-960.
- Bergström, R. & Hjeljord, O. 1987: Moose and vegetation interactions in northwestern Europe and Poland. - *Swedish Wildlife Research Supplement* 1: 213-228.
- Boutin, S. 1990: Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. - *Canadian Journal of Zoology* 68: 203-220.
- Boyce, M.S. 1989: The Jackson elk herd: intensive wildlife management in North America. - Cambridge University Press, Cambridge, 306 pp.
- Bubenik, A.B. 1998: Behavior. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); *Ecology and management of the North American Moose*. Smithsonian Institution Press, Washington, D.C. and London, pp. 1-733.
- Cederlund, G. 1982: Mobility response of roe deer *Capreolus capreolus* to snow depth in a boreal habitat. - *Swedish Wildlife Research* 12: 39-68.
- Cederlund, G., Sandegren, F. & Larsson, K. 1987: Summer movements of female moose and dispersal of their offspring. - *Journal of Wildlife Management* 15: 342-352.
- Couturier, S. & Barrette, C. 1988: The behaviour of moose at natural mineral springs in Quebec. - *Canadian Journal of Zoology* 66: 522-528.
- Danell, K., Niemela, P., Varvikko, T. & Vuorisalo, T. 1991: Moose browsing on Scots pine along a gradient of plant productivity. - *Ecology* 72: 1624-1633.
- Doenier, P.B., DelGuidice, G.D. & Riggs, M.R. 1997: Effects of winter supplemental feeding on browse consumption by white-tailed deer. - *Wildlife Society Bulletin* 25: 235-243.
- Guillet, C., Bergström, R. & Cederlund, G. 1996: Size of winter home range of roe deer *Capreolus capreolus* in two forest areas with artificial feeding in Sweden. - *Wildlife Biology* 2: 107-111.
- Gundersen, H., Andreassen, H.P. & Storaas, T. 1998: Spatial and temporal correlates to Norwegian moose-train collisions. - *Alces* 34: 385-394.
- Heikkilä, R. & Härkönen, S. 2000: Thinning residues as a source of browse for moose in managed forests in Finland. - *Alces* 36: 85-92.
- Houston, D.B. 1968: The Shiras moose in Jackson Hole, Wyoming. - *Technical Bulletin*, 1, Grand Teton Natural History Association, 110 pp.
- Hundertmark, K.J. 1998: Home range, dispersal and migration. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); *Ecology and management of the North American Moose*. Smithsonian Institution Press, Washington, D.C. and London, pp. 303-335.
- Ims, R.A. 1987: Responses in the spatial organisation and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. Male spacing systems in microtine rodents. - *Journal of Animal Ecology* 56: 485-496.
- Irwin, L.L. 2002: Migration. - In: Toweill, D.E. & Thomas, J.W. (Eds.); *North American Elk: Ecology and Management*. Smithsonian Institution Press, Washington, pp. 497-508.
- Kilpatrick, H.J. & Stober, W.A. 2002: Effects of temporary bait sites on movement of suburban white-tailed deer. - *Wildlife Society Bulletin* 30: 760-766.
- Lääperi, A. 1990: Hoidettujen talvilaitumien vaikutus hirvituhoihin mäntytaimikoissa. (In Finnish with an English summary: Effect of winter feeding on moose damage to young pine stands.) - *Acta Forestalia Fennica* 212, 46 pp.
- Lavsund, S. 1987: Moose relationships to forestry in Finland, Norway and Sweden. - *Swedish Wildlife Research Supplements* 1: 229-244.
- LeResche, R.E. 1974: Moose migrations in North America. - *Le Naturaliste Canadien* 101: 393-415.
- Lewis, T.L. & Rongstad, O.J. 1998: Effects of supplemental feeding on white-tailed deer, *Odocoileus virginianus*, migration and survival in Northern Wisconsin. - *The Canadian Field-Naturalist* 112: 75-81.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. 1996: SAS systems for mixed models. - SAS Institute Inc., Cary, NC, 633 pp.
- Marchinton, R.L. & Hirth, D.H. 1984: Behavior. - In: Halls, L.K. & House, C. (Eds.); *White tailed deer: Ecology and Management*. Stackpole books, Harrisburg, 129-168 pp.
- Nicholson, M.C., Bowyer, R.T. & Kie, J.G. 1997: Habitat selection and survival of mule deer: Tradeoffs associated with migration. - *Journal of Mammalogy* 78: 483-504.
- Odden, J., Linnell, J.D.C., Støen, O.G., Gangås, L., Ness, E. & Andersen, R. 1996: Trekk og områdebruk hos elg i østre deler av Hedmark. (In Norwegian with an English summary: Migration and home range use by moose in eastern Hedmark: A study in connection with a proposed military training area in Østlandet.) - *NINA Oppdragsmelding* 415: 1-34.
- Ouellet, J-P., Crête, M., Maltais, J., Pelletier, C. & Huot, J. 2001: Emergency feeding of white-tailed deer: test of three feeds. - *Journal of Wildlife Management* 65: 129-136.
- Ozoga, J.J. & Verme, L.J. 1982: Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. - *Journal of Wildlife Management* 46: 271-301.
- Ozoga, J.J. 1972: Aggressive behaviour of white-tailed deer at winter cuttings. - *Journal of Wildlife Management* 36: 861-868.
- Peek, J.M., Schmidt, K.T., Dorrance, M.J. & Smith, B.L. 2002: Supplemental feeding and farming of elk. - In: Toweill, D.E. & Thomas, J.W. (Eds.); *North American Elk: Ecology and Management*. Smithsonian Institution Press, Washington, D.C. and London, 617-647 pp.
- Pulliainen, E. 1974: Seasonal movements of moose in Europe. - *Le Naturaliste Canadien* 101: 379-392.
- Sabine, D.L., Morrison, S.F., Whitlaw, H.A., Ballard, W.B., Forbes, G.J. & Bowman, J. 2002: Migration behavior of white-tailed deer under varying winter climate regimes in

- New Brunswick. - *Journal of Wildlife Management* 66: 718-728.
- Schmidt, K. 1993: Winter ecology of nonmigratory Alpine red deer. - *Oecologia* 95: 226-233.
- Schmitz, O.J. 1990: Management implications of foraging theory: Evaluating deer supplemental feeding. - *Journal of Wildlife Management* 54: 522-532.
- Schwartz, C.C. & Hundertmark, K.J. 1993: Supplemental feeding of moose during winter: Can hay serve as an emergency ration? - *Alces* 29: 135-148.
- Sinclair, A.R.E. 1983: The function of distance movements in vertebrates. - In: Swingland, I.R. & Greenwood, P.J. (Eds.); *The ecology of animal movement*. Clarendon Press, Oxford, pp. 240-258.
- Smith, B.L. 2001: Winter feeding of elk in western North America. - *Journal of Wildlife Management* 65: 173-190.
- Solberg, E.J. & Sæther, B-E. 1999: Hunter observations of moose *Alces alces* as a management tool. - *Wildlife Biology* 5: 107-117.
- Storaas, T., Gundersen, H., Henriksen, H. & Andreassen, H.P. 2001: The economic value of moose - a review. - *Alces* 37: 97-107.
- Sweaner, P.Y. & Sandegren, F. 1989: Winter range philopatry of seasonally migratory moose. - *Journal of Applied Ecology* 26: 25-33.
- Van Ballenberghe, V. 1977: Migratory behavior of moose in southcentral Alaska. - *International Congress of Game Biology* 13: 103-109.
- Veiberg, V., Loe, L.E., Myrsetrud, A., Langvatn, R. & Stenseth, N.C. 2004: Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? - *Oecologia* 138: 135-142.
- Wood, P. & Wolfe, M.L. 1988: Intercept feeding as a means of reducing deer-vehicle collisions. - *Wildlife Society Bulletin* 16: 376-380.