SEASONAL AND HABITAT DIFFERENCES IN VISIBILITY OF MOOSE PELLETS

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ABSTRACT: Counts of faecal pellet groups have been widely used to estimate population densities and trends of large ungulates like moose (*Alces alces*). The visibility of pellet groups affects the accuracy of estimates, decreases with time, and varies among habitat types. I investigated the impact of season and habitat type on how, over time, visibility of moose pellets decreased along a forest productivity gradient in boreal forests of northeastern Sweden. Visibility decreased at the fastest rate during the transition from spring to summer due to concealment by new vegetation. Visibility also varied significantly among habitat types and was correlated with vegetative litter production. After one winter of exposure, more than 95% of all pellet groups were visible independent of habitat type, but thereafter visibility decreased fast in more productive habitats. The results demonstrated that if study plots are cleared in late autumn after the vegetation period and then visited as soon as possible after snowmelt, pellet counts can be used to estimate population trends and habitat use of moose in winter without bias caused by differences in visibility within different habitat types. Also, the correlation with litter production suggests that if a sightability correction factor is developed, pellet counts could be used to estimate habitat use and population distribution during the vegetation period and with longer periods between plot visits.

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Counts of faecal pellet groups have been widely used to estimate population densities and trends of large ungulates (Wallmo et al. 1962, Neff 1968, Timmermann 1974, Harestad and Bunnell 1987). It is a less expensive technique than population estimates from aircraft (Härkönen and Heikkilä 1999) and might be more precise in forests with dense overstory vegetation (Jordan et al. 1993), although there are methodological problems (Neff 1968).

The visibility of pellet groups is an important factor affecting the estimates from pellet counts (Wallmo et al. 1962, Lehmkuhl et al. 1994), but is rarely attributed much importance (Harestad and Bunnell 1987, Aulak and Babinska-Werka 1990). Visibility decreases with time as a result of concealment by vegetation and decay processes. The commonly used "clearance-plot" method is based on faecal accumulation in previously cleared plots. Correcting for pellet groups which have become invisible between consecutive plot visits is critical for the reliability of the method (Massei et al. 1998).

How fast visibility decreases depends to a great extent on habitat type (Smith 1968, Lavsund 1975, Harestad and Bunnell 1987, Lehmkuhl et al. 1994, Massei et al. 1998). Visibility decreases faster in moister habitats with more vegetation than in dry habitats with scarce vegetation (Lavsund 1975, Harestad and Bunnell 1987, Lehmkuhl et al. 1994). Faster concealment in more vegetated habitats is suggested to be a primary factor contributing to observed differences in visibility of pellet groups (Harestad and Bunnell 1987), and vegetative litter is especially important (Lavsund 1975). The decrease of visibility also varies by season and decreases faster during the growing season and in autumn than in winter (Aulak and Babinska-Werka 1990, Massei et al. 1998).

There is a general lack of information on the fate of moose pellets, especially in areas where moose densities are high and where pellet counts could be an alternative to helicopter surveys and other methods of population estimation. My study objective was to estimate seasonal and habitat differences in visibility of moose pellets (i.e., the percentage of the original surface area of each pellet group still visible). More specifically, I tested how fast visibility decreased in spring, summer, and autumn respectively, if visibility was correlated to habitat productivity, and if some plants and substrates (i.e., the ground cover the pellet groups were lying on) contributed more than others to a decrease in visibility.

STUDY AREA

The study was done in the middle boreal zone (Ahti et al. 1968) of coastal northern Sweden (Fig. 1), at 8 sites (Table 1) situated 50 - 90 km north and north-west of Umeå (63°50' N, 20°18' E). The length of the vegetation period (average day temperature > 5° C) was 120 - 150 days with onset between 10 and 20 May. Yearly precipitation was 600 - 700 mm (Raab and Vedin 1996), and precipitation during the vegetation period was 300 - 350 mm (Nilsson 1996). Snow covered the ground approximately from 20 - 25 October to 5 - 15 May (Raab and Vedin 1996). All sites used in this investigation were young forest stands of Scots pine (*Pinus sylvestris*), interspersed with various deciduous trees; mainly birches (*Betula pubescens* and *B. pendula*), but also rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), and willows (*Salix* spp.). Raspberry (*Rubus idaeus*), wavy hair grass (*Deschampsia flexuosa*), blueberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*), heather (*Calluna vulgaris*), and fireweed (*Epilobium angustifolium*) were common. To prevent bias caused by differences in soil moisture among sites, the sites were selected to have as little slope as possible.

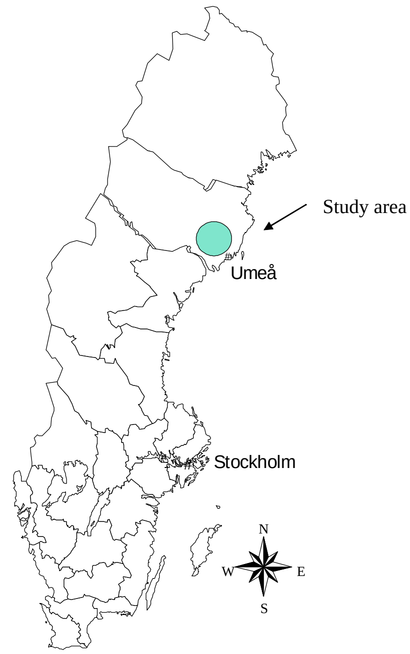

Fig. 1. Map of Sweden showing the study area.

METHODS

The study sites (Table 1) were selected to represent a forest productivity gradient, covering the range of forest types in the region (Hägglund and Lundmark 1987, Fridman et al. 2001). Site productivity was estimated as Site Index (estimated top height at 100 years) for Scots pine using methods developed for young forest stands (Lindgren et al. 1994, Elfving and Kiviste 1997). Site index is a common measurement of habitat productivity in forestry in Sweden (Persson

Table 1. Study sites ranked by increasing Site Index for Scots pine (mean top height in meters at 100 years). Litter production (g dry mass per m^2 and year; all treatment plots per exclosure pooled) estimated 2001-02 (Persson 2003), mean age of trees (years), geographic location (WGS84), altitude (m above sea level), and major tree species present.

Site	Site Index	Litter	Mean Age	Geographic Location	Altitude	Tree Species[1]
Lögdåberget	12.9	18.08	16	64° 00' N, 18° 45' E	300	B, P, Po, (S, Sa)
Skatan	14.7	15.85	9	64° 13' N, 19° 09' E	265	B, P, (Po, Sa)
Djupsjöbrännan	24.3	15.83	9	64° 06' N, 19° 12' E	250	B, P, Sa
Åtmyrberget	24.8	55.02	9	64° 12' N, 19° 17' E	305	B, P, S, Sa, (Po)
Selsberget	26.3	11.40	7	64° 15' N, 19° 16' E	175	B, P, S, (Po, Sa)
Mörtsjöstavaren	26.4	56.38	7	64° 22' N, 20° 07' E	280	B, P, S, Sa
Ralberget	27.3	27.15	9	64° 13' N, 20° 42' E	250	B, P, S, Sa, (Po)
Rönnäs	27.9	12.01	9	64° 02' N, 20° 40' E	62	B, P, (Po)

[1] B = *Betula* spp., P = *Pinus sylvestris*, Po = *Populus tremula*, S = *Sorbus aucuparia*, and Sa = *Salix* spp. Tree species occurring sparsely are in brackets.

2003). However, Site Index is developed for conifers, and studies have shown that conifers and hardwoods have fundamentally different soil-plant interactions (Ollinger et al. 2002). Litter production might be a better biological measurement of habitat productivity (Persson 2003). Thus, I also tested for relationships between the visibility of pellet groups and vegetation litter production in each plot.

The study of pellet visibility was done in connection with an experimental study, where browsing, defecation and urination of different levels of moose population density were simulated in 8 exclosures (i.e., the study sites) along a forest productivity gradient (Persson 2003). To simulate defecation, 39 pellet groups of 0.8 litres were laid out at each study site on 4 occasions (May 1999, October 1999, June 2000, and August 2000). The number of pellet groups was estimated based on defecation rates of moose (Persson et al. 2000). The pellet groups were deposited within circles of 35 cm in diameter and marked with a plastic stick in the centre. The moose pellets were collected from a nearby moose farm. Pellet groups showing clear evidence of decomposition were not collected. The animals were using mainly natural habitats and had free access to natural food (Nyberg and Persson 2002). It was thus an experimental study with pellet groups of equal size and origin.

Twelve randomly selected pellet groups from each of the 4 age classes of pellets (i.e., pellet groups laid out May 1999, October 1999, June 2000, and August 2000) were investigated at each site; 48 pellet groups per site and 384 for the whole study (one pellet group was not found in spring and some others were not found in summer and autumn; the total *n* was therefore 383 in spring, 376 in summer, and 371 in autumn). The reason for the missing pellet groups was that some markers were accidentally kicked down by fieldworkers during the experimental treatment.

The same pellet groups were investigated in spring (21 - 31 May), in summer (16

- 20 July), and after the vegetation period (22 - 31 October) in 2001.

At each visit, visibility (from standing position) was estimated to the nearest 5%. All pellet groups which became invisible disappeared due to concealment by vegetation, not as a result of decay. No signs of other wildlife having disturbed the pellet groups by scratching in search for insects or nematodes were found.

The relationships between visibility and Site Index, as well as litter production, were checked. Percentage of the different plants which covered the pellet groups either by growing over them or by litterfall was visually estimated to the nearest 5%, and classified as lichens, mosses, grasses, forbs, dwarf shrubs, raspberry, ferns/horsetails, and litter. Because there were few values for some plant groups, site differences were only tested for the most common groups. Ground cover was recorded as lichens, mosses, grass, or bare ground.

Data were analysed statistically using the SAS System for Windows (version 8.2, 2001). The Kruskal Wallis test was used to test for differences in visibility among study sites, plants concealing the pellet groups, and substrate types (Siegel and Castellan 1988). Correlations between visibility, Site Index, and litter production were checked using the Pearson correlation coefficient (Fry 1999) or (if the assumptions for a parametric test failed) the Spearman correlation coefficient (Siegel and Castellan 1988). When significant correlations were found, linear regression models were developed. The significance level was set at α = 0.05.

RESULTS

The mean visibility (the percentage of the original surface area of each pellet group visible) decreased with time (Fig. 2). The largest decrease in visibility was 10% per month, and occurred during the transition from spring to summer after one winter (9 months of exposure). Thereafter, visibility decreased at a slower rate.

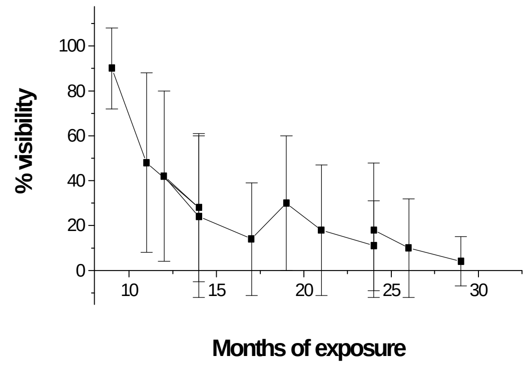

Fig. 2. The change in percent visibility (mean and standard deviation) with time of moose faecal pellets, all study sites pooled.

The mean visibility differed significantly among study sites for all seasons: (spring: Kruskal Wallis test, χ^2 = 100.92, P < 0.001; summer: χ^2 = 174.25, P < 0.001; and autumn: χ^2 = 149.60, P < 0.001; df = 7 in all tests, Fig. 3). No correlations were found between the mean visibility and Site Index for all pellet groups pooled or for spring, summer, and autumn respectively for pellet groups laid out in 1999 and 2000 combined (Spearman r, P > 0.16 for all tests) or pellet groups laid out in 2000 (P > 0.07 for all tests). However, there were significant negative correlations between mean visibility and litter production for pellet groups laid out in 1999 and 2000 (Fig. 4a), which could be described by linear regressions (Table 2). For pellet groups laid out in 2000 there was a trend, although not significant, that the mean visibility of all pellet groups pooled decreased with litter production (Fig. 4b). Significant negative correlations were also found between litter production and visibility of pellet groups investigated in spring, summer, and autumn, respectively (Table 2).

The relative proportions of plant groups concealing pellet groups differed signifi-

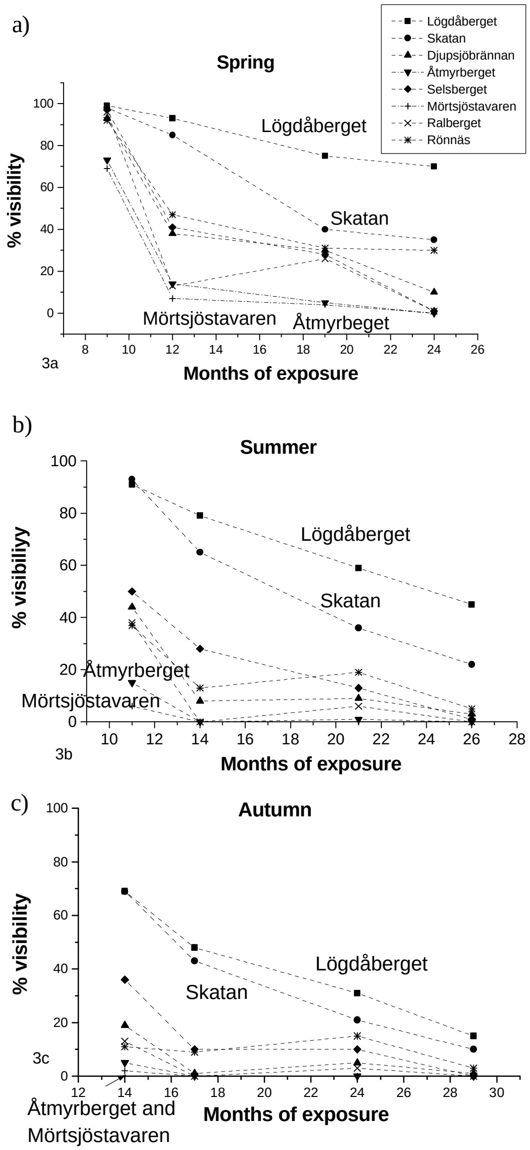

Fig. 3. The mean visibility of moose faecal pellets at different study sites ranked according to Site Index, investigated in spring (a), summer (b), and autumn (c).

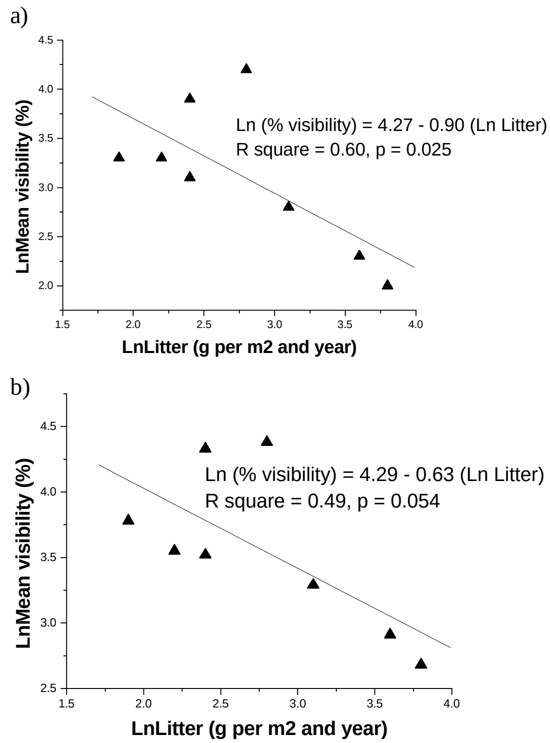

Fig. 4. The negative correlation between mean visibility (%) and habitat productivity estimated as litter production (g dry mass per m^2 and year): (a) all faecal pellet groups and investigations pooled for pellet groups laid out in 1999 and 2000, exposed for an average of 18 months; and (b) all pellet groups and investigations pooled for pellet groups laid out in 2000, exposed for an average of 12 months.

cantly among study sites for all seasons (Table 3, Fig. 5). Grasses contributed most to the concealment in all seasons, and at all study sites except Lögdåberget and Skatan. Mosses were also important in all seasons and at all study sites, whereas lichens only were important at Lögdåberget and Skatan. Åtmyrberget and Mörtsjöstavaren had the richest field vegetation, and in addition to grass, raspberry, forbs, ferns, and horsetails covered the pellet groups at those sites in summer, whereas litter was important in autumn.

The visibility of pellet groups differed significantly among substrate types for all seasons: (spring: Kruskal Wallis test, χ^2 = 73.61, P < 0.001; summer: χ^2 = 128.44, P < 0.001; and autumn: χ^2 = 114.44, P < 0.001; df = 2 in all tests, Fig. 6). Only 4 pellet groups were on barren ground, and because low sample size makes statistical tests unreliable, these groups were omitted from the analysis. Visibility was highest on lichen substrate and lowest on grass. The difference among substrate types was

Table 2. Statistics from the regression models (F, P, and R^2) describing correlations between mean visibility (%) of faecal pellet groups and vegetative litter production (g dry mass per m^2 and year) for pellet groups laid out in 1999 and 2000 combined, as well as in 2000. The regressions are estimated as ln visibility = ln litter for all pellet groups and investigations pooled for each site ("Total"), as well as for all pellet groups at each site of the investigations in spring, summer, and autumn 2001, respectively.

	1999 and 2000	2000
Total	$F = 8.84, P = 0.025, R^2 = 0.60$	$F = 5.69, P = 0.054, R^2 = 0.49$
Spring	$F = 9.34, P = 0.022, R^2 = 0.61$	$F = 8.01, P = 0.030, R^2 = 0.57$
Summer	$F = 12.08, P = 0.013, R^2 = 0.67$	$F = 8.88, P = 0.023, R^2 = 0.60$
Autumn	$F = 13.41, P = 0.011, R^2 = 0.69$	$F = 8.00, P = 0.030, R^2 = 0.57$

higher in summer and autumn than in spring: In summer and autumn, the mean visibility was 13 - 16 times higher for pellet groups lying on lichen than on grass, whereas visibility was 3 times higher in spring. Visibility was 4.5 - 5 times higher for pellet groups lying on moss than on grass in summer and autumn, and only 1.7 times higher in spring.

DISCUSSION

My study demonstrated that visibility of moose pellets decreased considerably with time. As a result of concealment by new vegetation, the largest decrease occurred in the transition from spring to summer after one winter of exposure. There were large habitat differences in how fast visibility decreased. I found no correlations between visibility and Site Index, whereas visibility was negatively correlated with vegetative litter production. Litter production could therefore be used to predict how fast the visibility of pellet groups decreases. Composition of the ground cover vegetation was an important factor affecting the visibility of pellet groups. Visibility was highest on lichen-rich sites without grass (i.e., Lögdåberget and Skatan) and lowest on sites with rich field vegetation of grass, forbs, ferns, horsetails, and raspberry (i.e., Åtmyrberget and Mörtsjöstavaren).

Pellet groups disappeared as a result of

Table 3. Results of Kruskal Wallis test for statistical differences in the relative contribution of various plant groups concealing moose pellet groups among study sites. χ^2 and P-values are presented in the table, df = 7 for all tests. Forbs, shrubs, raspberry, ferns, horsetails, and litter (in summer) contributed less to the concealment and were omitted in the tests.

Vegetation	Spring (χ^2, P)	Summer (χ^2, P)	Autumn (χ^2, P)
Lichens	140.13, < 0.001	165.31, < 0.001	192.11, < 0.001
Mosses	14.13, = 0.049	26.51, < 0.001	37.52, = 0.005
Grass	139.80, < 0.001	139.80, < 0.001	192.11, < 0.001
Litter	161.97, < 0.001	-	207.59, < 0.001

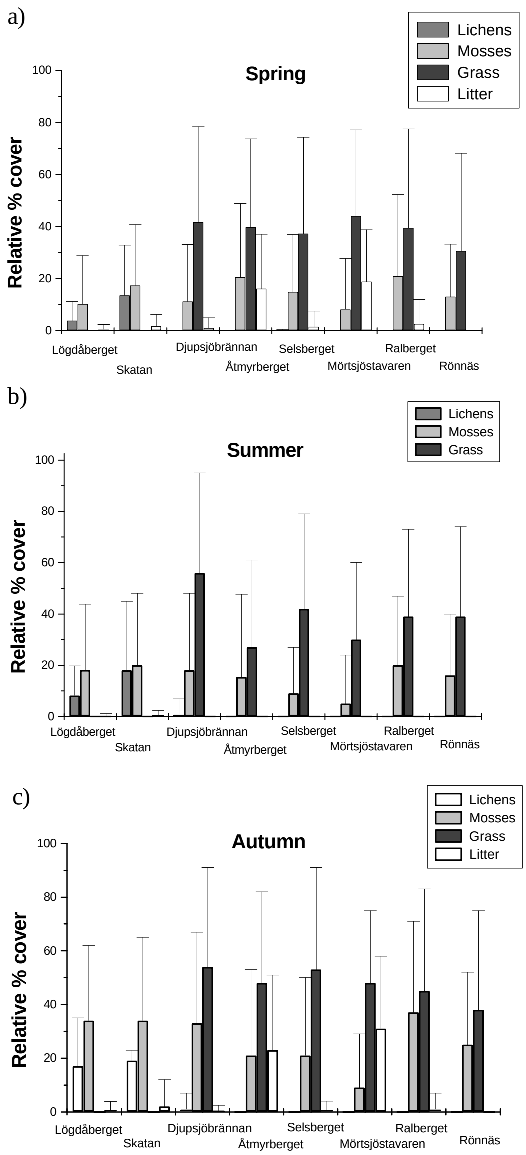

Fig. 5. The relative contribution (mean and standard deviation) of the most important vegetation types concealing moose faecal pellet groups at different study sites ranked after Site Index; investigated in spring (a), summer (b), and autumn (c). Forbs, shrubs, raspberry, ferns, horsetails, and litter (in summer) contributed less to the concealment and were omitted in the figures.

concealment by vegetation rather than decay processes. Studies from Vancouver Island, British Columbia (Harestad and Bunnell 1987), and the Olympic Peninsula,

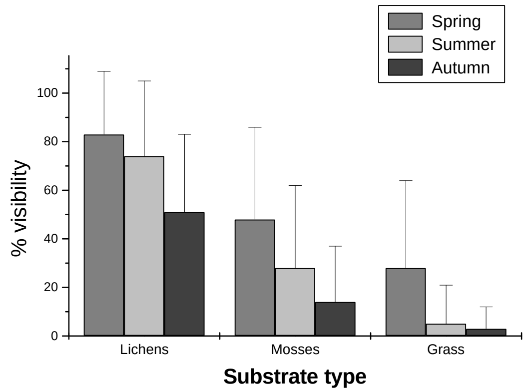

Fig. 6. The visibility (mean and standard deviation) of moose faecal pellets lying on different substrate types, all study sites pooled.

Washington (Lehmkuhl et al. 1994), have reported the opposite. However, their studies were done in areas with milder climate and higher annual precipitation. The relatively cold and dry climate in my study area was probably the main explanation for lower decay rates. Vegetation concealment likely results in higher moisture which increases decomposition rate and decreases visibility in more moist and vegetated habitats (Lehmkuhl et al. 1994). It is likely that the sites with the richest field vegetation also offered the moistest conditions at ground level.

Reliable methods to estimate population density, habitat use, and distribution of moose are important for wildlife and forest management (Härkönen and Heikkilä 1999). Unless pellet counts are done immediately after snow melt before green up, one needs to know how fast visibility decreases, and habitat differences must be regarded. After one winter of exposure, more than 95% of the deposited pellet groups were visible (i.e., visibility > 0 from standing position) independent of habitat type in the study area. Population trends and habitat use by moose in winter can thus be estimated without biases caused by visibility differences in boreal forest habitats with a relatively dry and cold climate. Because of the fast decline in visibility after the first winter, it is important to clear the study plots in late autumn after the vegetation period and then visit them as soon as possible after snowmelt. However, moose have different food preferences in summer and winter (Cederlund et al. 1980, Bergström and Hjeljord 1987), and habitat use and distribution of moose in the vegetation period is also interesting to reveal for moose managers. The correlations between visibility and litter production suggest that visibility can be estimated as a function of habitat productivity. More studies of the relationship between visibility and habitat productivity should be done to establish a sightability correction factor for various habitat types. The pellet count method could then be used to estimate habitat use and population distribution in the landscape during the vegetation period and with longer periods between plot visits.

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