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Habitat selection by moose (*Alces alces*) in southwestern Sweden

Älgars habitatval i sydvästra Sverige

Biology
D-level thesis

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Abstract

The moose (*Alces alces*) is very important both economically and ecologically, therefore all knowledge of moose is vital for future management of the moose population. Little is known about moose habitat selection in Sweden. In coastal southwestern Sweden growing human population and new infrastructure projects continuously threaten to fragment and isolate local moose populations. The habitat selection of 22 moose, 8 males and 14 females, in southwestern Sweden was studied from February 2002 until December 2005. The moose were captured and fitted with GPS-collars and positions were collected at 2-hour intervals. The number of moose positions totaled 71103 during the study period of 46 months. Data for individual animals were divided into four seasons: spring, summer, fall and winter based on climate and moose biology. A total of 125 moose seasonal home ranges were generated and habitat use within each of the generated home ranges was studied using Euclidean distance-based analysis. A reclassified digital landcover map was divided into the land use classes agriculture, clear-cut, coniferous forest, deciduous forest, mire and mountain. The results showed that there was a difference in habitat selection between males and females. Males were significantly closer to forest and clear-cuts compared to females. Both males and females selected clear-cuts and avoided agriculture within their home ranges.

Sammanfattning

Älgen är en viktig art, både ekonomiskt och ekologiskt, och all kunskap är viktig för att även i framtiden kunna sköta en sund älgstam. Trots flertalet studier finns det många frågetecken om älgens habitatval i Sverige. En ökad exploateringstakt och nya infrastrukturprojekt hotar att fragmentera och isolera populationer av älg. Habitatvalet hos 22 älgar, 8 tjurar och 14 kor, i sydvästra Sverige studerades mellan februari 2002 och december 2005. Älgarna sövdes och utrustades med GPS-sändare, deras positioner registrerades varannan timma och det totala antalet positioner under den 46 månader långa studietiden var 71103 stycken. Data från varje älg delades in i 4 säsonger; vår, sommar, höst och vinter, baserat på klimat och älgens biologi. Totalt genererades 125 hemområden baserade på säsong, och valet av habitat inom varje hemområde studerades med hjälp av Euclidean distance-based analysis. En omklassificerad digital marktäckedata användes som var indelad i 6 olika klasser; odlad mark, hygge, barrskog, lövskog, myrmark och berg i dagen. Resultaten visade att det var skillnad mellan könen i hur de väljer habitat. Tjurarna var signifikant närmare barrskog och hyggen än korna, men både tjurar och kor selekterade för hyggen och undvek odlad mark inom deras hemområden.
Introduction
The Moose (Alces alces) is one of the most important wildlife species in Sweden, both economically and ecologically. It is of great value to hunters, both for the meat it produces and for the recreational value. It is important ecologically since it affects, in some cases negatively, the vegetation of the forest landscape. Further, it is important as a risk factor in traffic; 4000 - 5000 moose-vehicle collisions occur every year and these cause on average 10 casualties (Vägverket 2006, Nationella viltolycksrådet (SES) 2007). Thus, a good management of the Swedish moose population is of great importance, and in order to achieve that, detailed information of habitat selection is needed. The possibility to use GPS collars in wildlife research has opened new opportunities for detailed study of how wild animals use their habitats. GPS collars have earlier been used in a number of studies of wildlife. In Sweden, wolves (Canis lupus), brown bears (Ursus arctos), ospreys (Pandion haliaetus) and honey buzzards (Pernis apivorus) have been equipped with GPS collar for research of their daily movements (Hake et al. 2003, Sand et al. 2004, Jansson 2005, Alerstam et al. 2006).

The Fennoscandian (Norway, Sweden and Finland) moose population is one of the most productive and most harvested in the world, which can be largely attributed to modern forestry techniques. A large quantity of clear-cuts has provided moose with large and well distributed areas of early successional stages of good habitats (Lavesund et al. 2003). This has supplied moose population with an infinitely supply of food (Lavesund 2003, Nikula et al. 2004). Moose management often relies on population level, but with GPS-collars the individual moose become the sampling unit (Jansson 2005).

Knowing which habitats animals use is vital for understanding their natural history and ecology. For this reason, it is not surprising that a number of different methods for studying habitat use have been developed (Conner et al. 2002). Habitat selection is a measure of how they use the habitats compared to availability. The knowledge of animal habitat selection and the use of habitat within home ranges are important in wildlife management, and especially among harvested game species. Home range is defined as the area a moose uses for its activity during a certain period of time (Cederlund and Sand, 1994). Within home ranges, moose find palatable food and also its social connections to other moose. The area suitable for an animal shall contain resources such as food, cover from predators and water. Moose are assumed to optimize important factors within their home range, both in a coarser and at a finer scale. At a coarser scale, food and protection from predators is the most important factors. At a finer scale, moose are thought to select habitats that are optimizing their food intake in different area depending on seasons (Courtois et al. 2002).

Sexual segregation can be divided in several categories depending on what the study is focusing on. This study is limited to sexual differences in habitat use which will be called habitat segregation (Conradt 1999, Conradt et al. 1999, Bowyer 2004). Sexual difference in use of habitat is defined as habitat segregation and is widespread in sexual dimorphic ungulates (Conradt et al. 1999, Bowyer 2004). This difference is important for the management of the moose population. It is well known that home range size differs between sexes in moose (Cederlund and Sand 1994), but it is more difficult to
predict what influence this has to habitat use. For example, males and females among
dimorphic ungulates have been reported to be so different in their space use and habitat
selection that they almost behave as two separate species (Bowyer and Kie 2004). Moose
have home ranges that often overlap other moose (Cederlund and Okarma 1988) and they
don’t defend territories. In these home ranges, moose use some areas to a higher extent
(core areas) than other areas included in the home range. This can cause differences
among gender in their choice of core areas for maximizing the nutritional intake
(Cederlund and Sand 1994). Females are known to use areas of higher quality whereas
males often use larger areas of poorer quality, but with a large quantity (Miller and
Litvaitis 1992). The theoretical reason for this pattern is that the larger males require less
food in relation to the body size. Thus, males don’t have the same demand on the quality
in their home range that females have (Mysterud 2000). The data was processed to
evaluate differences in sex and season in their habitat use, using third order habitat use
according to Johnson (1980).

The objectives of this study were to analyze seasonal habitat selection among males and
females, e.g. if there was a difference between moose gender in their choice of habitat
within their seasonal home ranges? I also analyzed moose habitat selection within home
range (third order selection (Johnson 1980)) in southwestern Sweden in order to examine
if there is a difference in habitat use between genders.

My hypotheses were that males and females selects habitat nonrandomly within their
seasonal home ranges and males and females do not select different habitat within their
home ranges.

Material and methods
The study was conducted in southwestern Sweden along European highway 6 (E6) north
of Uddevalla. E6 stretches along the Swedish west coast from Trelleborg in the south to
the border of Norway, all way through Norway to Kirkenes at the border of Russia. The
road from Trelleborg in Sweden to Oslo in Norway is under reconstruction and converted
from a two lane nonfenced road to a fenced four lane highway. The 15 km highway that
divides the study area in two equal sized fragments has been converted in two stages; the
southern section was finished in June 2000 and the northern in June 2004. Since there
was concern that the moose population on the peninsula west of the highway would be
isolated when the fenced highway was complete, three wildlife crossings were built, two
overpasses and one underpass.

The study area is defined by the localization of the fenced highway and the minimum
convex polygon method (Mohr 1947) of all non-migratory GPS-collared moose positions
(see data analysis below). Elevation within the study area ranged between 0 – 169 m
above mean sea level. The study area included two biogeographical regions, the
boreonemoral and the nemoral region (Abrahamsen et al. 1977) divided by 15 km of the
E6. The 30 000 ha study area east and west of E6 differed in their land use composition.
The area east of the highway was within the boreonemoral zone, the area west within the
nemoral zone, and the highway divides the study area in two equal sized land areas.
The two sides of the road are rather different in their appearance. The mature coniferous forest dominated the landscape east of the highway (61%) with a low amount of deciduous forest (9%), farmland (7%), mire (6%), water (4%), glade (2%) and human development (1%). The landscape west of the highway was dominated by a mosaic of mature coniferous forest (32%), farmland (31%), deciduous forest (11%) and glade (12%) with a low amount of human development (3%), water (0.8%) and mire (0.2%). The amount of clear cut forest are equal (10%) on both sides of the highway. Norwegian spruce (Picea abies) and Scots pine (Pinus sylvestris) dominate the boreal forests, with a weft of deciduous species as common alder (Alnus glutinosa), oak (Quercus robur), birch (Betula pendula & Betula pubescens) and mountain ash (Sorbus aucuparia). Agricultural lands were comprised of crops that primarily included wheat (Triticum aestivum), barley (Avena sativa), oats (Hordeum vulgare), and rye (Secale cereal), as well as hay and pastureland composed of a mosaic of grasses that commonly included perennial rye (Poa pretensis), quackgrass (Elytrigia repens), orchardgrass (Dactylis glomerata), tufted hairgrass (Deschampsia cespitosa), and timothy (Phleum pretense).

Figure 1. The highway E6 study area with wildlife passages (solid dots) from south to north: highway overpass Grytingen completed June 2000, highway underpass Myren completed June 2000, and highway overpass Hogstorp completed June 2004. Open dots indicate capture locations of the 24 collared moose. Circles indicate mean composite (at least one year of data) home ranges of male (52.2 km²) and female (15.6 km²) moose calculated with minimum convex polygon method (MCP).
Moose capture and data collection
As part of a larger study of interactions between moose and traffic, a total of 24 moose, 9 males and 15 females, were captured and fitted with GPS-collar (Televilt inc.) from February 2002 until December 2005. They were captured and collared within a 5500 ha area transected by the highway. Moose positions were collected at 2-hour intervals and the number of moose positions totaled 71103 during the study period of 46 months. Each moose was collared up to 22 months (Mean=17.0; Min=3; Max=22; Std. Dev.=8.0) before collars fell off due to preprogrammed drop-off mechanisms. Data for individual animals were divided into four seasons based on climate (SMHI, National database) and moose biology (Pulliainen, 1974; Cederlund and Okarma, 1988); Spring: 16 March – 15 May. Summer: 16 May – 30 August. Fall: 1 September – 30 November. Winter: 1 December – 15 March.

Data analyses
A reclassified digital landcover map were used and was divided into 6 general land use classes; agriculture, clear-cut, coniferous forest, deciduous forest, mire and mountain. An area that is cultivated was characterized as agriculture. Clear-cut is an area that ranges from a clear-felled area to early successional forest up to 5 m in height. Mountain is an upper elevated area with very thin soil or flat rock areas (Appendix 1).

The positions from 22 moose (8 males and 14 females) were transferred into ArcView 3.3 (ESRI, Redlands, California) and analyses of habitat selection were made. Two moose were excluded from analysis, one due to a migratory behavior and one because of collar failure. It was possible to determine nonrandom habitat use by comparing simulated random points within each moose seasonal home range with actual locations. A home range was generated when more than 50 positions within a season were available, generating a total of 125 moose seasonal home ranges using minimum convex polygon method. All 6 general land use classes were included in all seasonal home ranges.

The data was processed to evaluate differences in sex and season in their habitat use, using third order habitat use according to Johnson (1980). Animal movement extension (Hooge and Eichenlaub 2000) were used to generate 1000 random points within each moose seasonal home range (n=125), and to generate 1000 random points in every moose composite (total) home range (n=22). The nearest feature extension (Jenness Enterprises 2004) was used to determine the distance from all positions (random and actual) to each of the 6 habitat classes. Euclidean distance-based analysis of habitat use relies on simulate distances from animal locations to habitat. The mean distances from animal locations to habitats were then divided with mean distances from simulated random points.

Statistics
A multivariate analysis of variance (MANOVA) was used to test the hypothesis that moose, female and male, did not select habitat at random. Further a multivariate analysis of variance (MANOVA) was used to test the hypothesis that overall habitat selection did not differ from random with sex as main effects and individual moose as the experimental unit. If the MANOVA test showed statistical significance for the two sexes, a univariate
t-test was made to determine which habitats were used disproportionably, one analysis for each sex. Habitat types with distance ratios significantly <1 were viewed as preferred, and those significantly >1 as avoided. Habitat types were ranked by performing pairwise mean comparisons using univariate t-tests (Conner and Plowman 2001, Perkins and Conner 2004). Differences in selection within each habitat among the four seasons were analyzed using Kruskal-Wallis by ranks and multiple comparisons (z-values) of the four seasons within each habitat were calculated to examine where seasonal differences appears. All analyzes were made in Statistica 7.1 and results were considered significant at p<0.05.

**Result**

The two sexes had different preference in habitat selection (MANOVA; $F_{6,112}=3.46$, $p=0.004$) within home ranges, however no seasonal (MANOVA; $F_{18,317}=1.32$, $p=0.13$) or sex x season (MANOVA; $F_{18,317}=0.91$, $p=0.57$) effect could be found. Differences in habitat selection among males and females were found in forest (t-test $t=-2.94$; $p=0.004$) and clear-cuts ($t=2.15$; $p=0.034$) (fig. 1), males were significantly closer to both forests and clear-cuts than females.

![Figure 1: Habitat selection among males and females all years and all seasons. The mean distances from animal locations to habitats are divided with mean distances from simulated random points. Habitat types with distance ratios significantly < 1 were preferred, and those significantly > 1 were avoided.](Diagram.png)

No differences could be found in deciduous forest ($t=1.44$; $p=0.15$, $N_1=41$, $N_2=84$), agriculture ($t=-0.094$; $p=0.92$), mountain ($t=-0.82$; $p=0.42$) or mire ($t=0.25$; $p=0.81$). Since a difference was found, males and females were handled separately in further analyses.
There was a significant difference in selection of forest (ANOVA H (3, N= 84) =12,05; p =0,0072) between seasons (fig. 2). The effect appears in spring vs. fall (z=2,74; p=0.037) and spring vs. winter (z=2,9; p=0.022). The seasons were then pooled to evaluate differences in selection among habitats.

![Figure 2: Females’ habitat use based on distant to nearest feature in different season. The mean distances from animal locations to habitats are divided with mean distances from simulated random points. Habitat types with distance ratios significantly < 1 were preferred, and those significantly > 1 were avoided.](image)

Females preferred some habitats and avoid some habitats (differed significantly from 1) within their home range. Females preferred clear-cut (t=-4,8; p<0.001, N=83), but avoided mire (t=2,75: p=0.0073, N=83) and agriculture (t=4,62; p<0.001, N=0,83) within their seasonal home range. No selection could be found for deciduous forest (t=-1,85; p=0.068, N=83), mountain (t=1,32; p=0.19) or boreal forest (t=0,35; p=0.73). A difference in preference was found for clear-cuts compared to deciduous forest and agriculture was significantly more avoided than mires (Table 1).

Table 1: Habitat types ranked from most to least preferred for third-order habitat selection by moose in Southwestern Sweden with Euclidean distance ratios indicated in parentheses. “>” indicates a rank-order difference with p>0.05 and “>>” indicates p<0.05. Habitat types in bold had a distant ratio that differed significantly (p<0.05) from 1.00.

<table>
<thead>
<tr>
<th>Ranking</th>
<th>Female</th>
<th>CC (0.84)</th>
<th>DFO (0.95)</th>
<th>MO (0.96)</th>
<th>FO (0.98)</th>
<th>MI (1.07)</th>
<th>AG (1.21)</th>
</tr>
</thead>
<tbody>
<tr>
<td>*</td>
<td>CC-clear cuts and young forests, FO-mature boreal forest dominated by Norwegian Spruce and Scotch Pine, MO-high elevated mountainous areas with scarce vegetation, DFO-mature deciduous forest, MI-mires, AG-agriculture.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
There was a significant difference in selection of agriculture (H (3, N= 41) =11.18; p =0.011) between seasons (fig. 3). The effect appears in spring vs. summer (z=3.12; p=0.01). The seasons were then pooled to evaluate differences in selection among habitats.

![Figure 3: Males’ habitat use based on distant to nearest feature in different season. The mean distances from animal locations to habitats are divided with mean distances from simulated random points. Habitat types with distance ratios significantly < 1 were preferred, and those significantly > 1 were avoided.](image)

Males preferred some habitats and avoided some habitats (differed significantly from 1) within their home ranges. Males preferred forest (t=-4.94; p<0.001, N=40) and clear-cut (t=-8.49; p<0.001, N=40), but avoided agriculture (t=3.62; p<0.001, N=40) within their home range. No selection could be found for mountain (t=-1.84; p=0.073), deciduous forest (t=0.47; p=0.64, N=40) or mire (t=1.35; p=0.19, N=40). A difference in preference was found for clear-cuts compared to mountain and agriculture was significantly more avoided than mires (Table 2).

![Table 2: Habitat types ranked from most to least preferred for third-order habitat selection by moose in Southwestern Sweden with Euclidean distance ratios indicated in parentheses. “>” indicates a rank-order difference with p>0.05 and “>>” indicates p<0.05. Habitat types in bold had a distant ratio that differed significantly (p<0.05) from 1.00.](image)
Discussion

Both males and females selected clear-cuts and avoided agriculture within their home ranges. Deciduous forest, mire, and mountain were all used close to random. Contrary to my main hypothesis, sexual segregation does occur. There is a difference between males and females in habitat selection. Males were found significantly closer to forest and clear-cuts compared to females.

Sexual segregation among ungulates is not something new. Earlier studies have related this to habitat segregation among sexes due to differences in home range size (Bowyer and Kie 2004). Males have larger home ranges than females (Cederlund and Sand 1994), and thus, males may have a more varying habitat structure within their home-range compared to females. Females’ home ranges are smaller and therefore include smaller total area of poor habitats. Since forest constitutes a high proportion of female’s home ranges, they might not use it more than random. Other habitats are found in lesser extent and thus, a preference or avoidance for a certain habitat might appear more obvious in the analyses.

Previous studies have shown that home range size differs between sexes in moose (Cederlund and Sand 1994), males have larger home ranges than females. Males have lower demand on the food quality within the home range, but because of the larger home range size, the food availability is sufficient (Cederlund and Sand 1994). This may have consequences in male habitat use and result in segregation among males and females in the selection of different habitats (Miller and Litvaitis 1992).

Females selected forest significantly more during spring than during fall and winter and they avoided agriculture during all seasons but especially in spring. Mature forest was used more during spring compared to fall and winter, which was contrary to previous studies. Hjelhjord et al. (1990) addressed the importance of mature coniferous forest to moose in late winter, and hypothesized that the delayed phenological changes in preferred food plants were the main reason for this pattern. Females preferred clear-cut within their home-range but there was no significant difference among seasons in the use of clear-cut. In this study females preferred clear-cut but avoided mire and agriculture within their home ranges. In addition they use deciduous forest and mountain a little bit more than random. Among females forest was used near random during all seasons except for spring. Females have smaller home ranges than males do (Cederlund and Okarma 1988). But food within their home ranges appears to be of higher quality than males and therefore it may not be a problem with food availability (Miller and Litvaitis 1992, Cederlund and Sand 1994).

Males significant avoided agriculture throughout the year. Also, the only significant effect of seasonal differences in habitat use of males is in agriculture where a significant effect appears in spring vs. summer. Males used agriculture more during summer than spring. During summer, agricultural fields primarily with oat often attract moose and may be an important and nutritious food resource (Ekman et al. 1993).
Males significantly select forest and clear-cut within their home ranges. Unlike females, males selected forest all year but with a slightly larger use during spring than the rest of the year. Both males and females used clear-cuts more than random, and males used clear-cuts significantly more than females. Contrary to previous Fennoscandian studies (Nikula et al. 2004), moose in this area selected clear-cuts and early successional forest equally throughout the year. They did not use clear-cut and early successional forest more during winter compared to other seasons. The importance of early successional forest habitats is earlier described in previous studies in Fennoscandia (Cederlund and Okarma 1988, Nikula et al. 2004). Nikula et al. (2004) observed pronounced more use of early successional pine-dominated plantation by both sexes during winter compared to summer. In this study, pine and spruce dominated clear-cuts and early successional forests were not separated, which might infer the seasonal results.

The use of Euclidean distances on position data has mostly been restricted on relations to points or linear habitat types (Clark et al. 1993, Boal and Mannan 1998, Jorgensen et al. 1998, McKee et al. 1998, Ormsbee and McComb 1998). Euclidean distances to habitats have not been given the same attention (Conner and Plowman 2001, Conner et al. 2003), even if more studies recently have started. Problems with Euclidean distance-based analysis, EDA, seem to occur when the home range size differs too much, as it does in this case. Dussault et al. (2005) question the applicability of EDA when different habitats do not have the same patch size. This is similar to the problem that was experienced in this study since the problem theoretically might occur when male and female home range differs in size. Females have smaller home ranges and therefore they have smaller patches with deviant habitats while males have larger patches with deviant habitats and therefore have a lot more distances that influence the statistical result. It would be interesting to compare the habitat use results from this method to the results from other methods (e.g. classification based analysis). One advantage with the EDA is that objects not included within home ranges also could be analyzed. A highway, a town or a creek, for instance could be avoided even though it is not included within the home range. Other methods have the limitation that those comparisons only could be done if the habitat is present within the home range.

Acknowledgments
I would like to thank Per Widén, the supervisor of this project. Special thanks to my assistant supervisor Mattias Olsson, who with his never failing enthusiasm made this project possible. I would also like to thank Lars Henrik Henriksson and the other students in computer lab 5D305, for creating a funny and lively atmosphere.
Reference


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Appendix 1. Reclassification scheme of landcover maps used to analyze moose habitat selection in Southwestern Sweden, from 2002-2005.

<table>
<thead>
<tr>
<th>Reclassified landcover category</th>
<th>Original landcover category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>Coniferous forest 5-15 m, not on lichen-rich ground</td>
</tr>
<tr>
<td></td>
<td>Coniferous forest &gt;15 m, not on lichen-rich ground</td>
</tr>
<tr>
<td></td>
<td>Coniferous forest &gt; 15 m, on lichen-rich ground</td>
</tr>
<tr>
<td></td>
<td>Coniferous forest on mire</td>
</tr>
<tr>
<td></td>
<td>Mixed forest on mire</td>
</tr>
<tr>
<td></td>
<td>Mixed forest, not on mire</td>
</tr>
<tr>
<td></td>
<td>Mixed forest, not on glade</td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>Deciduous forest on mire</td>
</tr>
<tr>
<td></td>
<td>Deciduous forest, not on mire</td>
</tr>
<tr>
<td></td>
<td>Deciduous forest, not on glade</td>
</tr>
<tr>
<td>Mountain</td>
<td>Glade and boulder-rich ground</td>
</tr>
<tr>
<td></td>
<td>Coniferous forest (&lt; 30% coverage) on glade</td>
</tr>
<tr>
<td></td>
<td>Deciduous forest (&lt; 30% coverage) on glade</td>
</tr>
<tr>
<td>Clear-cut</td>
<td>Early successional forests 0-5 m high</td>
</tr>
<tr>
<td></td>
<td>Clear-cut</td>
</tr>
<tr>
<td>Mire</td>
<td>Wetland</td>
</tr>
<tr>
<td></td>
<td>Mire</td>
</tr>
<tr>
<td>Agriculture</td>
<td>Pasture</td>
</tr>
<tr>
<td></td>
<td>Arable land</td>
</tr>
<tr>
<td></td>
<td>Not urban park</td>
</tr>
<tr>
<td></td>
<td>Golf course</td>
</tr>
</tbody>
</table>