Forest Ecology and Management 419–420 (2018) 170–178

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Forage availability and moose winter browsing in forest landscapes

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ARTICLE INFO

Keywords:
Browsing
Forage
Ideal free distribution
Landscape
Moose

ABSTRACT

In a large-scale survey, comprising 38 landscapes throughout Sweden, we measured winter forage availability and use by moose within different forest- and land types, and also at three different spatial scales: plot, tract and area.

Measured as percent cover of browse species within moose browsing range, young forests contained significantly more browse (16.5 ± 1.20%: mean ± SE) compared with older forests (6.7 ± 0.57%) or non-forest land (5.9 ± 0.67%). Total cover of browse species increased with increasing mean tree height in forests, and peaked at around 22% when the trees were 3–5 m. The relative consumption was highest in young forests (9.2 ± 0.98%) compared with non-forest land (7.8 ± 1.40%) or older forests (5.8 ± 0.78%). The selection order did not vary much among forest- or land types, with aspen, willows, rowan and oak being the most selected species.

A multiple regression, including four independent variables (moose index, cover of Scots pine, cover of other species and temperature sum) explained 45% (young forests), 18% (older forests) and 36% (non-forest land) of the variation in relative consumption. In young forests, moose index and cover of Scots pine accounted for 40 and 44%, respectively, of the explained variation. Model selection, using AICc, further emphasized the importance of moose index and cover of Scots pine, as these variables were included in the most parsimonious models for all forest- and land types.

At the tract level, we recorded a proportional relationship between total cover of browse species and absolute consumption, suggesting an ideal free distribution. Taking into account the availability of forage, the degree of browsing and the proportion of each land type in the landscape, we calculated that 44.3% of the total forage consumption occurred in young forests, 42.3% in older forests and 13.4% in non-forest land.

Our main conclusions are that moose conform to an ideal free distribution based on availability of forage within the landscape, and that all forest- and land types, not just young forests, are important as sources of browse for moose. Thus, it may be possible to release the browsing pressure on damage-sensitive young forests by increasing the food supply in other forest- and land types. Furthermore, managers needs to consider both the size of the moose population and the amounts of browse in the landscape when deciding on prudent management actions.

1. Introduction

The distribution of animals in relation to available resources is one of the fundamental questions in ecology (Morris, 2003). According to the optimal foraging theory, animals should select to forage in patches that return the highest net energy (Charnov, 1976). Other feeding strategies may involve, e.g., maximizing intake of protein (Mattson, 1980) or minimizing intake of plant secondary metabolites (Freeland and Janzen, 1974; Langvatn and Hanley, 1993). However, external factors such as weather, seasonality or predators may also influence herbivore foraging decisions, resulting in altered foraging patterns (e.g., Senft et al., 1987; Laundré et al., 2010).

The ideal free distribution is one of the basic concepts regarding frequency-dependent distribution of a single animal species (Fretwell

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https://doi.org/10.1016/j.foreco.2018.03.049
Received 15 January 2018; Received in revised form 22 March 2018; Accepted 24 March 2018
Available online 30 March 2018

and Lucas, 1970). In its basic form, this optimal foraging model assumes that animals are ideal (omniscient, i.e., have perfect knowledge of resource profitability), equal competitors and free (can move freely between resources at no cost). If this is the case, animals will distribute themselves in relation to the available resources. In a log - log presentation of availability and consumption of a resource, this will manifest itself as a proportional relationship, i.e., the slope of a regression line will be equal to one. If the assumptions are met, deviations from one could mean that resources are over- or underused or that there is a bias in the utilization due to biotic or abiotic constraints, such as presence of predators or variation in local climate (Kennedy and Grey, 1993). There has been much debate on whether or not observed animal distributions actually conform to the ideal free distribution (e.g., Kennedy and Grey, 1993; Grey and Kennedy, 1994; Milinski, 1994), but later studies show some support of this theory (see Křivan et al., 2008 and references therein).

In Sweden, moose (*Alces alces* L.) use a variety of food plants, although a limited number of browse species normally makes up the bulk of the food (Shipley, 2010). During winter conditions, woody plants such as trees and shrubs constitute the majority of browse (Cederlund et al., 1980). The deciduous species rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.) and willows (*Salix* spp.) are ranked among the most selected species by moose, followed by juniper (*Juniperus communis* L.) and silver birch (*Betula pendula* Roth), in turn followed by Scots pine (*Pinus sylvestris* L.) and downy birch, *Betula pubescens* Ehrh. (Månsson et al., 2007b). Although ranked intermediate with regard to selection, the conifer Scots pine is quantitatively the most important winter food species for moose in Sweden (Bergström and Hjeljord, 1987).

Earlier studies regarding moose browsing have typically targeted young forests and, especially, Scots pine (e.g., Bergqvist et al., 2001, 2014). However, moose also utilize browse in other forest or land types (e.g., Månsson, 2009). Environmental conditions may affect chemical and/or morphological features in browse species and, hence, the suitability as food for moose. For instance, Scots pine trees growing in young stands differ in their chemical composition compared with trees of the same species growing in a less productive environment, such as under a canopy of other trees, and this subsequently affects browsing levels (Danell et al., 1991).

In this study, we were interested in determining the availability and use of winter browse for moose in different forest- and land types, particularly in relation to the theory of ideal free distribution. Our main hypothesis was that an ideal free distribution, if present, would manifest itself mainly within the landscape (i.e. at the tract level) where a single moose may actually have knowledge of the available resources and move around freely, something that is generally not possible among landscapes (areas) due to distance. The alternative hypothesis was that other, biotic or abiotic, variables were of higher importance for the distribution of moose than were food resources. Such circumstances would result in alternative relationships, which likely cannot be interpreted on scales of food resources and consumption. Furthermore, we wanted to calculate a gross estimate of the total forage consumption by moose in each forest- or land type. For this, we used a large-scale survey material collected throughout Sweden. This material is rare, because it includes data on forage availability and consumption in different types of forested habitats, as well as at different ages of production forests.

2. Materials and methods

The study encompassed 38 areas (landscapes) across Sweden with the aim of covering a wide range of environmental conditions and moose population densities, Fig. 1. We stratified the sampling in order to cover as many counties as possible, with a random distribution within county. Spanning a range in latitudes from 56°N to 67°N, forest landscapes in the nemoral as well as the hemi-boreal and boreal vegetation zones were included (sensu Ahti et al., 1968). Based on latitude and altitude we calculated a temperature sum (day degrees) for each area (Morén and Perttu, 1994), Table 1. Temperature sum generally decreases from south towards north and from lower to higher altitudes, and reflects the local growing conditions. We also used it as a proxy to characterize the location of an area in the country.

Throughout Sweden, the winter of 1991/1992, preceding the survey, was milder and with less snow than normal. The North Atlantic Oscillation (NAO) index for January–March 1992 was around 0.8 units above the 1950 – 2000 base period mean (National Weather Service, 2015) and the mean temperature for Sweden during December 1991–February 1992 was almost 2 °C above the 1900–1999 mean value (SMHI, 2015). Thickness of the snow cover was approximately 80% and length of the period with snow approximately 85% compared to 10-year mean values (Wern, 2015).

2.1. Large herbivore species

Out of the four large herbivore species found in Sweden: moose, roe deer (*Capreolus capreolus* L.), red deer (*Cervus elaphus* L.) and fallow deer (*Dama dama* L.), moose was the only species present in all study areas. The total moose harvest was around 113,000 animals in the autumn of 1991, equivalent to approximately 0.3 moose km^{-2} (Liberg et al., 2010). Based on harvest figures, we estimated the moose population in the winter of 1991/92 at 0.6–1.4 animals km^{-2}, however with large regional variations.

At the time, roe deer populations were dense in the southern part of the country. No reliable population estimates were available for roe deer, but a generalized map of roe deer population densities published a few years after the study indicated 10–20 animals km^{-2} (Cederlund and Liberg, 1995). Red deer and fallow deer occurred only as discrete small populations (total harvest 1991/92 around 500 for red deer and 2000 for fallow deer: Liberg et al., 2010). Hence, in the northern study areas, moose was the sole browsing agent whereas roe deer may have contributed to the browsing in the southern areas.

2.2. Survey areas

In the south (areas 1–22) each study area was 9 × 7 km, whereas 9 × 10 km areas were used in the north (areas 23–38: Table 1, Fig. 1). The smaller area size in the south was due to landscapes being generally more heterogeneous in that part of the country, compared with landscapes further north. Within each study area, 20 quadratic tracts (16 in area 25), each 1 × 1 km, were positioned in a systematic way, Fig. 1. Hence, a total of 756 tracts were established.

A total of 20 circular plots (hereafter denoted standard plots) were established along the circumference of each tract at a distance of 200 m between plots (Fig. 1), giving a total of 15,120 standard plots. In addition, an extra plot was established between two standard plots (at exact distance of 100 m from each) if the plot fell within forests with a tree mean height of 0.5–5 m. In total, 1614 extra plots were established in the 38 study areas. The position of each plot centre was determined using a compass and step counting.

Field work was performed by professional foresters and game keepers representing the respective landowners. All people involved were experienced in this type of work and attended a one-day course before the survey. Field work was conducted during the spring of 1992, commencing directly after snow-melt and finishing before bud flush, i.e. at different times during the spring depending on location.

2.3. Field measurements

Each standard plot was assigned to one of six land types: forests, mires, open bedrocks, water, arable fields and grazing land, or other land. Mires and open bedrocks are low-productive land, i.e. with an expected annual forest production of less than 1.0 m^3 ha^{-1} $year^{-1}$ whereas forests have an expected annual forest production of 1.0 m^3 ha^{-1} $year^{-1}$ or more. Other land may be power lines or forest-road