1 **Title:**

2 Cascading effects of moose (*Alces alces*) management on birds

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26

1   **Abstract**

2   Large herbivores often have key functions in their ecosystems, and may change

3   ecosystem processes with cascading effects on other animals. The mechanisms often

4   involve relocations of resources of various kinds, including reduction in resource

5   availability following large herbivore foraging and increase in resources from animal

6   excreta. As large herbivore populations in Europe generally are intensely managed,

7   management activities may interact with the activities of the herbivores themselves in

8   the effect on other ecosystem components. We investigated the effects of moose (*Alces*

9   *alces*) winter browsing, together with the effect of net nutrient input via supplementary

10   winter feeding of moose on functional composition and species richness of birds in a

11   boreal forest. Supplementary feeding stations for moose had a net zero effect on bird

12   species richness and abundance, because negative effects of moose browsing were

13   balanced by positive effects of nutrient input. Sites with a similar browsing intensity as

14   at feeding stations but without nutrient input had lower abundance and species richness

15   than feeding stations. Functional groups of bird species showed differing responses:

16   Birds nesting at or below browsing height were negatively affected by moose browsing,

17   whereas species nesting above the browsing zone were positively affected by moose

18   browsing. Insect eating species responded negatively to moose browsing on birch but

19   positively to nutrient input at feeding stations, whereas seed eating species responded

20   positively to birch browsing and negatively to feeding stations. This study showed that

21   both high levels of cervid activity and human management interventions influenced the

22   bird community.

23

1 Introduction

2

3 Large herbivores often have key functions in their ecosystems (Hobbs 1996). They have

4 the potential to directly and indirectly influence growth and structure of individual

5 plants and plant parts, population dynamics, composition and succession of plant and

6 animal communities, as well as fundamental ecosystem processes like nutrient cycling

7 (Danell *et al.* 2003; Hester *et al.* 2006; Hobbs 1996; Pastor *et al.* 2006; Persson *et al.*

8 2000; Skarpe and Hester 2008; Suominen *et al.* 2008). The high density of cervids in

9 Europe, North America and Japan during recent decades has raised concern about how

10 this may affect ecosystem components such as bird species diversity in temperate and

11 boreal forests (Allombert *et al.* 2005; Côte *et al.* 2004; Fuller 2001; McShea and

12 Rappole 2000; McShea *et al.* 1997; Miyashita *et al.* 2004). During recent decades, the

13 Fennoscandian moose (*Alces alces*) populations have increased to densities that have

14 probably not been experienced in post-glacial time (Cederlund and Bergström 1996). A

15 large herbivore such as the moose can modify the environment for other species by its

16 selective feeding, trampling, urination and defecation (Berger *et al.* 2001; Melis *et al.*

17 2007; Pastor *et al.* 1993; Persson *et al.* 2000; Suominen *et al.* 2008). Ecosystem effects

18 on other animals and long-term effects are poorly known (Suominen and Danell 2006),

19 and there is a need for research on cascading effects of high densities of cervids on

20 different animal taxa.

21

22 Supplementary feeding is a management tool used to increase winter survival of

23 cervids, reduce damage to forest plantations and minimise ungulate – vehicle collisions

24 (Gundersen *et al.* 2004; Luccarini *et al.* 2006; Putman and Staines 2004; Weisberg and

25 Bugmann 2003). Supplementary feeding of moose with silage during winter is common

1 in Norway, and leads to extremely high moose densities locally around feeding stations

2 (Gundersen *et al.* 2004). Supplementary feeding also constitutes a local net input of

3 nutrients directly from feed remains and indirectly via animal dung and urine. The high

4 moose density and nutrient input may be expected to have cascading effects on the

5 ecosystem locally around feeding stations.

6

7 High ungulate densities can affect diversity and abundance of birds by modifying

8 habitat structure and food resources (Fuller 2001; Suominen and Danell 2006). Moose

9 browsing in boreal forest may lead to a reduction of deciduous trees, which are

10 important for many bird species (Stokland 1997) and to a more open canopy (Persson *et*

11 *al.* 2000) which may increase predation risk (Martin and Joron 2003) and reduce

12 availability of nesting sites (Allombert *et al.* 2005; Berger *et al.* 2001; DeCalesta 1994;

13 McShea and Rappole 2000). Some studies of moderate browsing have shown positive

14 effects on invertebrates (Danell and Huss-Danell 1985), constituting an important food

15 resource for many bird species, but high browsing pressure over long time periods is

16 usually negative for invertebrate abundance (Stewart 2001; Suominen *et al.* 2008). Also

17 seed production, important for seed eating birds, may respond to browsing (Bergström

18 and Danell 1987). While moose browsing in boreal forest may reduce resource

19 availability (Pastor and Naiman 1992; Persson *et al.* 2007; Persson *et al.* 2005b),

20 supplementary feeding of moose brings resources into the system with potential positive

21 effects on productivity. Nutrient input may affect plant production, chemistry and the

22 way the trees respond to browsing by compensatory growth (Danell *et al.* 1997; Persson

23 *et al.* 2007), which in turn may have effects on invertebrate fauna or seed production

24 and hence food availability for birds. The forage provided for moose may also contain

25 seeds or insects that contribute directly to food availability for birds.

26

4

1   We investigated the effects of long-term supplementary winter feeding of moose on the

2   community of small to medium-sized birds in a boreal forest system in South-East

3   Norway. The distribution of moose around supplementary feeding stations in winter

4   makes it possible to study gradients in moose winter browsing and net input of

5   nutrients. Both herbivory and nutrient input can have positive, negative or unimodal

6   effect on species richness (Mackey and Currie 2001; Waide *et al.* 1999). Since moose

7   densities around feeding stations are very high (van Beest *et al.* 2010), and nutrient

8   availability in boreal forest is generally low (Bonan and Shugart 1989), we expect

9   negative effects of moose browsing and positive effects of nutrient input on bird species

10   richness. The aim of this study was to test if moose browsing generally has negative

11   effects on bird species richness and abundance, and if different functional groups of

12   birds may respond differently. However, at feeding stations we may have effects of both

13   moose browsing and input of nutrients. This leads to 3 possible scenarios:

14

15   1) Feeding stations have a negative effect on bird species richness and abundance,

16   because negative effects of moose browsing are stronger than positive effects

17   of nutrient input.

18   2) Feeding stations have a net zero effect on bird species richness and abundance,

19   because negative effects of moose browsing are balanced by positive effects

20   of nutrient input.

21   3) Feeding stations have a positive effect on bird species richness and abundance,

22   because effects of nutrient input are stronger than browsing effects.

23

Materials and methods

Study system

This study was carried out in Stor-Elvdal municipality, Hedmark County in southeast Norway (~61°N, 11°E). The study area is situated between 291 and 684 m.a.s.l. in the middle and northern boreal vegetation zone (Moen *et al.* 1999). The area is dominated by a main river valley running northwest - southeast, interspersed by side valleys and mountainous areas. The forest in this area consists of pure or mixed stands of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), downy birch (*Betula pubescens)* and silver birch *(Betula pendula*) interspersed with species such as grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willows (*Salix* spp.). Most of the forest is managed for commercial production of timber or pulp. The field layer vegetation is often dominated by dwarf shrubs such as cowberry (*Vaccinium vitis-idaea*) and bilberry (*V. myrtillus*). Data from weather stations in the valley bottom from the last 30-year period show a mean summer temperature of 10.6 $^{\circ}$C (May-September) and mean winter temperature of -5.8 $^{\circ}$C (October – April). During the same period, the mean annual precipitation was 628 mm and the mean snow depth 39 cm (eKlima 2008). The bird community in the area is typical for a Scandinavian boreal forest, dominated by migratory species such as the chaffinch (*Fringilla coelebs*) and willow warbler (*Phylloscopus trochilus*) in summertime, and more resident species such as Eurasian siskin (*Carduelis spinus*) and tit species (*Parus* spp.) in the winter, with occasional peaks in drifting species such as crossbills (*Loxia* spp.).

The moose population in the area is mainly migratory, spending the summer at higher altitudes and migrating down to the valley bottom where the snow depth is lower in

1   winter. The landowners have carried out organised supplementary winter feeding of

2   moose with grass silage since 1990 (Gundersen *et al.* 2004), to reduce traffic accidents

3   and damage to young pine stands. On average around 600 (± 140 SE) tonnes of silage is

4   provided each year in Stor-Elvdal municipality, increasing over the last 10 years (Stor-

5   Elvdal landowner association, unpubl. data). In the winter 2006-2007, before this study

6   was carried out, approximately 778 tonnes silage were deposited at feeding stations in

7   the municipality. This equals an average of 63-78 kg nitrogen per feeding station. The

8   effects of the nutrient input can be observed locally around feeding stations, by an

9   increase in herbaceous vegetation growth and flowering and in presence of nitrogen-

10   demanding species in the field-layer vegetation (Torgersen 2008). The feeding stations

11   are mainly placed along forest roads in the side-valleys. The overall moose density in

12   the municipality is about ~1,1 moose per km^2 (Gundersen *et al.* 2004), but in winter the

13   effective moose density is many times higher in the valley bottom. In 2007 when this

14   study was carried out, moose density at 1 km distance from feeding stations was 3.6 ± 1

15   moose pr km^2 (estimated from pellet counts (this study, see methods) assuming 14

16   pellet groups per moose per day in winter (Persson *et al.* 2000) and a winter period of

17   180 days). At a local scale of 25-50 meters radius around feeding stations, pellet group

18   density corresponded to a moose density of 130 ± 20 moose /km^2, however, this reflects

19   intensive use of feeding stations by moose, rather than population density in the area.

20

21   **Field procedures**

22   We performed replicated point counts of birds at 11 supplementary feeding stations for

23   moose and 11 control sites. Point counts are appropriate for comparisons of relative

24   densities between habitats (Bibby *et al.* 2000) and feeding stations represent points of

25   high moose density and input of nutrients in the landscape. The feeding stations used in

26   this study had been in use for more than 10 years, thus reflecting long-term effects on

1   the ecosystem. The control sites were selected in similar vegetation types as the feeding

2   stations, with similar elevation (290-680 m.a.s.l.) (Table 1) and distance to forest roads,

3   and all controls had a minimum distance of 1 km from any feeding station. All sites had

4   a nest box for small birds that was used in a parallel study on reproduction, which might

5   lead to a somewhat higher occurrence of hole-nesting species in this survey than is

6   otherwise common for this type of forest. However this was similar for feeding stations

7   and controls.

8

9   The study was carried out between early May and mid-June 2007. Each site was visited

10   5 times during the study period, approximately once a week. All sites were visited on

11   the same day between 04:30 and 08:30 a.m. Days with wind or heavy rain were

12   avoided. The 3-4 observers and the time of day were rotated systematically among sites

13   and sampling days to avoid bias due to observer or time of day. All observers had

14   previous experience with observing birds, and were trained on bird species common for

15   this region. During observation, all vocalisations of territorial males were counted for

16   10 minutes, as an indicator of the relative abundance of breeding territories. The song of

17   bird species that carried further than 1 km would be recorded at both feeding stations

18   and controls, but this would not affect the analysis. As the effects of feeding stations are

19   quite local in scale (Gundersen *et al.* 2004), we expected effects on species with small

20   home ranges, and this study was designed to detect local-scale differences in relative

21   density.

22

23   For all sites that were used in bird counts we recorded habitat variables in May-June as

24   follows: Moose pellet groups were counted in 5 circular plots of 50 m^2, one plot at the

25   observation point and four plots 25 m from the observation point in each of the

26   directions north, south, west and east. Only pellet groups from last winter were counted.

1   The age of the pellet group was determined on basis of pellet colours/moisture and

2   cover of leaf litter (Neff 1968). Moose browsing pressure was estimated as % browsed

3   shoots of shoots available at browsing height (0.5 – 3 m) in the same plots. We

4   estimated browsing pressure on trees of birch, pine and spruce separately, and other

5   species (rowan, aspen, willow, alder) were grouped together because of their low

6   densities. In addition, we surveyed vegetation variables in July, in a circular plot of 10

7   m radius around the observation point, to give a rough estimate of the vegetation type,

8   similar to the relevé method (Almendinger and DNR 2007). These variables were: %

9   vertical canopy cover of trees with total height below and above 3 m for birch, pine,

10   spruce and other species (grouped) and % ground cover of the categories herbs, lichens

11   and dwarf shrubs. The sites were categorised by forest vegetation type (Moen *et al.*

12   1999): 1 = lichen forest, 2 = cowberry-bilberry forest, 3 = heather bog-bilberry pine, 4 =

13   bilberry forest and 5 = small-fern forest. The age of the forest was categorised according

14   to Norwegian forestry cutting classes: 1 = clearcut, 2 = trees up to 8 m height, 3 = trees

15   higher than 8 m, but not mature, 4 = forest mature for cutting, 5 = old growth forest.

16

17   **Statistical analyses**

18

19   **Comparison of habitat at controls sites and feeding stations**

20   To ensure that control and feeding station sites were similar in vegetation type, and

21   different in moose activity, we compared browsing, pellet group density and habitat

22   variables between all feeding stations and controls with an ANOVA (or Kruskal-Wallis

23   for non-normally distributed variables) using SAS software (SAS-Inst. 2003). Feeding

24   stations and control sites had similar vegetation types, elevation and canopy cover of

25   tree species, indicating that control sites were appropriate (Table 1). Birch browsing

26   (%), spruce browsing (%), pellet groups density and % herb cover were significantly

1　higher at feeding stations compared to controls, and % cover of dwarf shrubs was

2　significantly lower, indicating a higher level of moose activity at feeding stations

3　compared to controls (Table 1). However, variation in birch browsing pressure was high

4　within control sites (Table 1). Pine browsing was 90 - 100% both at feeding stations and

5　controls, but sample size of plots containing pine was too small for a reliable test

6　between feeding stations and controls.

7

8　**Analysis of species richness and abundance**

9　We tested for differences in bird species richness and abundance between feeding

10　stations and controls with ANOVA using the average of all 5 replicates per station.

11　Hypothesis testing of control versus feeding stations showed no significant differences

12　in bird species richness or abundance. We therefore further used model selection to

13　investigate which habitat- and methodological variables were important in explaining

14　bird species richness and abundance, using the selection criteria AICc (corrected Akaike

15　Information Criterion) (Burnham and Anderson 2002) and among models with ΔAICc <

16　2 we selected the most parsimonious model (the model with the fewest model terms)

17　(Quinn and Keough 2002). The minimum adequate model was then used to evaluate the

18　effect of feeding stations on species richness and abundance.

19

20　We investigated the effects of observer, date and time of day and habitat variables on

21　species richness and abundance in a mixed model with repeated design (station/date)

22　with poisson distributed errors using the GLIMMIX macro in SAS software (SAS-Inst.

23　2003). We chose several candidate models by selecting the most relevant habitat

24　variables (see below) and analysing several combinations of these (Table 2). The

25　explanatory variables analysed were date, time, observer, feeding treatment (control,

26　feeding station), % birch browsing, cutting class, and vegetation variables (see below).

1   We investigated the relationship between explanatory variables with simple correlations

2   to avoid including highly correlated variables (Graham 2003). As spruce browsing and

3   moose pellet density were strongly correlated with feeding treatment, they were not

4   included in the model. Pine browsing was not included in the model because of low

5   occurrence of pine within browsing height and low variation in browsing pressure.

6   Therefore birch browsing was the variable that represented the gradient in moose

7   browsing intensity best. For the categorical variables with many levels, such as date,

8   observer and cutting class, we first did pair-wise comparisons using Scheffé corrections

9   within the full model, to see which levels were significantly different from others, and

10 then grouped the levels that were not significantly different, to reduce the number of

11 parameters.

12

13 To include all the vegetation variables measured, but avoid intercorrelation, we did a

14 principal component analysis (PCA) of all vegetation variables (tree cover, field

15 layer/ground cover and vegetation type), and included the sample scores of PCA axis 1

16 and 2 in the model. Axis 1 was positively correlated with herbs and vegetation type 5

17 (small-fern forest) and negatively correlated with dwarf shrubs, representing the

18 gradient between richer vegetation types with herbs/grasses and poorer vegetation types

19 with cowberry/bilberry woodland. Axis 2 was positively correlated with cover of spruce

20 > 3 m high and negatively correlated with lichen cover, representing the gradient from

21 spruce to lichen/pine forest.

22

23 For the variables such as observer, date and time of day, we first investigated if they had

24 any effect in a linear model of species richness/abundance including all the variables.

25 Species richness varied among observation days ($F_{4,79} = 3.27$, $p = 0.016$), but with no

26 consistent trend in time. Species richness also varied among observers ($F_{4,62} = 6.95$, p=

1   0.0001) and time of day ($F_{1,79} = 7.84$, $p = 0.0064$). However, because observers and

2   time of the day were systematically rotated among sites and days of observation, this

3   did not lead to any visible bias in the results. These variables were included in further

4   modelling, to account for the effect of observer, date and time. Total abundance of

5   territorial males showed the same variation with time, date and observer as species

6   richness did.

7

8   **Analysis of functional groups and individual species**

9   All bird species were grouped into functional groups (Appendix 1) according to

10   migratory strategy (migratory/resident/drifting), main feeding ecology in the

11   observation period (insects/seeds/buds, woodpeckers forming a separate group) and

12   nesting height (below, at and above 0.5-3 m browsing height for moose) (Cramp 1977),

13   to see if functional groups differed in response to feeding treatment and habitat

14   variables. Investigation of abundance of groups according to diet/migration and their

15   relation to habitat variables was analysed by ordinations in the statistical software

16   package Canoco (ter Braak and Smilauer 2006). Linear response models were used, as

17   the gradient determined by the first axis of a detrended correspondence analysis (DCA)

18   was below 4 standard deviations (Hill and Gauch 1980). For each site we used the mean

19   number of singing males of each group across the 5 sampling days to relate species

20   abundance to environmental variables. We carried out a principal component analysis

21   (PCA) and a redundancy analysis (RDA) to investigate functional group composition

22   and relation to environmental variables. The significance of environmental variables in

23   explaining abundance of functional groups was tested with Monte Carlo permutation

24   tests in a RDA in Canoco. Ordinations are not as sensitive to intercorrelated variables as

25   a normal regression analyses, so we included most of the environmental variables

1   measured, but removed the environmental variables that were highly correlated with

2   other variables in the analysis.

3

4   The environmental variables that contributed to explaining the variation of functional

5   group abundance in ordinations were further explored for each functional group in a

6   mixed model with poisson distributed errors using the GLIMMIX macro in SAS (Littell

7   2006). Instead of using a repeated design, we used the mean abundance over 5 sampling

8   events, and added the number of the observation site as a random intercept. The

9   abundance of nesting height groups was analysed only with linear models in SAS, as

10 there were only 3 groups.

11

12 We analysed the individual bird species response to habitat variables with the same

13 linear methods in Canoco as for functional group abundance. In ordinations we

14 excluded species that were observed only once (Appendix 1), so that rare species should

15 not dominate in the ordination.

Results

Effects of moose browsing and feeding stations on total species richness and abundance

We recorded a total of 32 species of male territorial birds (Appendix 1). Bird species richness and abundance showed no difference when comparing feeding stations and controls alone using ANOVA (richness: $F_{1,20} = 0.15$ $p = 0.70$, abundance : $F_{1,20} = 0.16$ $p = 0.69$ Figure 1a). However, the large variation in browsing pressure on controls made it possible to analyse the effects of browsing and of feeding stations separately (Figure 1 b). The minimum adequate model for species richness included the variables birch browsing, feeding station/control, observer (grouped) and vegetation-PCA axis 2 (Table 2). Species richness decreased with increasing birch browsing, but species richness was higher at feeding stations than at controls with equally high browsing pressure (Table 3 and Figure 1b). At the control sites, species richness decreased from 7.4 (± 1.1 SE) to 4.8 (± 1.0 SE) species per site (- 35 %) when birch browsing increased from 10 % to 95 % (Figure 1b), whilst species richness at feeding stations was 0.81(± 1.0 SE) species per site higher (+ 17%) than at controls. Species richness was positively correlated with vegetation-PCA axis 2, representing a positive correlation with spruce forest or a negative correlation with lichen/pine forest. The variables that best described the abundance of territorial males included feeding station/control, birch browsing, observer and date (grouped) (Table 3). Abundance of territorial males showed the same pattern as species richness (Figure 1 c). Abundance decreased from 9.3 (± 1.1 SE) birds per site at 10 % browsing pressure to 6.5 (± 1.1 SE) at 95 % browsing pressure at controls (-30%), but was 0.84 (± 1.1 SE) birds per site higher (+ 13%) at feeding stations compared to controls.

1

Response of functional groups to birch browsing and feeding stations

An RDA of the abundance in different functional groups selected the following

variables by Monte Carlo tests (including 999 permutations): birch browsing (F = 2.22,

p = 0.092), % cover of pine less than 3m high (F = 2.26, p = 0.092), feeding station (F =

2.35, p = 0.058) and cutting class 2 (F = 2.13, p = 0.088), together explaining 37 % of

the variation in bird species composition. From interpretation of the PCA diagram

(Figure 2a) we could identify two main modes of reaction to birch browsing: seed-eaters

were positively correlated with birch browsing, whilst the insect-eaters were negatively

correlated with birch browsing, and mixed seed-insect eaters were in an intermediate

position (Figure 2a). There was no clear pattern between groups with different

migration strategy (Figure 2a). All functional groups seemed to be negatively correlated

with cover of small pine, and strict insect eating groups were most abundant in cutting

class 2 (Figure 2a). The same patterns can be observed in the ordination of individual

species (Figure 2b).

As functional groups with a similar diet (seeds/insects) responded in similar ways to

birch browsing in the ordination diagram, we grouped the bird species into larger

groups of seed- or insect-eaters, but excluded mixed seed-insect feeders because of their

intermediate position, and woodpeckers because of their different ecology. Then we

tested for an interaction between diet (seed/insect), feeding station and birch browsing.

There was a significant interaction between diet and the effects of both feeding station

($F_{1,19}$ = 8.31, p = 0.0095) and birch browsing ($F_{1,19}$ = 15.36, p = 0.0009) on abundance.

Insect eaters decreased in abundance with increasing birch browsing, but had a higher

abundance at feeding stations compared to controls, whilst seed eaters increased with

1   increasing birch browsing and had a lower abundance at feeding stations compared to

2   controls (Figure 3a).

3

4   Abundance of birds in the different nesting categories responded differently to birch

5   browsing, but not to feeding treatment ($F_{1,60} = 1.68$, $p = 0.120$). The interaction between

6   nesting group and birch browsing was significant ($F_{3,59} = 5.03$, $p = 0.0036$). Abundance

7   of birds nesting below browsing height and at browsing height decreased with

8   increasing birch browsing, whilst abundance of birds nesting above browsing height

9   increased with increasing birch browsing (Figure 3b).

10

11   **Responses of individual bird species to feeding stations and birch browsing**

12   Few species showed differences in abundance between feeding stations and controls,

13   except the pied flycatcher (*Ficedula hypoleuca*), which had a higher abundance at

14   feeding stations than at control sites (Appendix 1, Figure 2b). To control that the

15   positive effects at feeding stations were not just due to this species, we ran the analysis

16   of feeding groups and species richness again excluding the flycatcher, and the

17   interaction between feeding stations and abundance of insect/seed eaters was still

18   significant ($F_{1,119} = 6.59$, $p = 0.019$), and so was the positive effect of feeding stations

19   on species richness ($F_{1,18} = 4.08$, $p = 0.058$), although slightly weaker. In an RDA of

20   abundance of all bird species, selection with Monte Carlo permutation showed that only

21   the variables birch browsing ($F = 2.47$, $p = 0.024$) and cutting class 2 ($F = 2.04$, $p =$

22   0.036) contributed significantly in explaining the variation in species abundance. Birch

23   browsing explained most of the variation in species abundance (11 %), while feeding

24   station/control explained 4 % of the variation ($F = 1.31$, $p = 0.23$) once birch browsing

25   and cutting class 2 were added to the model. *Parus major* and *Phylloscopus trochilus*

26   were common far from feeding stations, most frequent in cutting class 2, and seemed to

16

1   be negatively correlated with birch browsing (Figure 2b). The seed-eater *Carduelis*

2   *spinus* was also most abundant far from feeding stations (Figure 2b). Insect-eaters

3   tended to be negatively correlated to birch browsing, except *Ficedula hypoleuca* and

4   *Regulus regulus* which may be positively correlated with birch browsing (Figure 2b).

5

Discussion

Feeding stations had a net zero effect on bird species richness and abundance in accordance with scenario 2, as negative effects of moose browsing on birch were balanced by positive effects of feeding stations (Figure 1abc). The positive effect of feeding stations was most likely caused by positive effects of input of nutrients to the ecosystem. Different functional groups of birds showed opposite responses to browsing and nutrient input; Insect eating species responded negatively to birch browsing but positively to nutrient input at feeding stations, whereas seed eating species responded positively to birch browsing and negatively to feeding stations. Birds nesting at or below browsing height were negatively affected by moose browsing, whereas species nesting above the browsing zone were positively affected by moose browsing.

Negative effects of heavy browsing or grazing by ungulates on abundance and species richness of birds have been documented in earlier studies (Fuller 2001; Suominen and Danell 2006), but these effects have mostly been linked to changes in vegetation structure (Allombert *et al.* 2005; Berger *et al.* 2001; DeCalesta 1994; McShea and Rappole 2000) whilst our results indicate that reduced food resources for insectivorous birds may also be an important mechanism. Although heavy or long-term browsing pressure seems to have negative effects on bird diversity, low or short-term grazing pressure can in some ecosystems have a positive effect on bird diversity (Loe *et al.* 2007). The positive effect of nutrient input at supplementary feeding stations on bird species richness is unique to this study. Folkard and Smith (1995) showed that fertilisation in boreal forest can have positive effects on bird abundance, probably due to increased plant growth increasing arthropod availability.

1   We found that bird species nesting at and below browsing height were negatively

2   affected by birch browsing. Earlier studies have also identified nesting height as an

3   important factor explaining bird responses to browsing (Allombert *et al.* 2005; Berger *et*

4   *al.* 2001; Casey and Hein 1983; DeCalesta 1994; McShea and Rappole 2000). For birds

5   nesting at and below browsing height, browsing and trampling may lead to loss of

6   nesting sites. Moose browsing changes tree structure and opens up the canopy

7   (Mathisen *et al.* 2010; Persson *et al.* 2007; Persson *et al.* 2005a) and may increase nest

8   predation from avian predators (Martin and Joron 2003). However, the abundance of

9   birds nesting above browsing height was positively correlated with birch browsing.

10

11   The dominance of insect eating birds in the summer bird community in the area most

12   likely explains why the overall abundance and species richness of birds showed the

13   same response as the insect eaters. The negative correlation between abundance of

14   insectivorous birds and birch browsing suggests that moose browsing has a negative

15   effect on the food resources or foraging sites for insectivorous birds, and that they

16   choose their breeding habitat to avoid heavily browsed areas. Since many of the

17   insectivores nest at or under browsing height, we cannot separate the effect of birch

18   browsing on habitat structure from that on food availability. However, feeding stations

19   had a higher abundance of insectivorous birds than control areas with equally high

20   browsing pressure. The effect of feeding stations was not significant for nesting groups,

21   suggesting an effect of feeding stations on food availability. The explanation may be

22   that nutrient input through dung, urine and residual silage directly and/or indirectly

23   increased the availability of arthropod prey.

24

25   Previous studies have shown diverse effects of cervid browsing on abundance and

26   diversity of different arthropod groups (Danell and Huss-Danell 1985; Riipi *et al.* 2005;

1   Stewart 2001; Suominen 1999; Suominen *et al.* 2008), but heavy browsing is reported

2   to mainly have negative effects (Miyashita *et al.* 2004; Shimazaki and Miyashita 2002;

3   Stewart 2001; Suominen 1999; Suominen *et al.* 2008), especially on herbivorous insects

4   (Suominen and Danell 2006). Moose browsing may reduce arthropod availability

5   through reduced birch leaf biomass (Pedersen *et al.* 2007; Persson *et al.* 2007), changed

6   chemical content (Danell and Huss-Danell 1985) or changed tree species composition

7   (Pastor and Naiman 1992). Few studies have investigated the link between browsing,

8   invertebrates and insectivorous birds, but Bailey and Whitham (2003) have

9   experimentally shown that elk (*Cervus canadensis*) browsing on aspen can reduce

10   abundance of galling sawflies, arthropod availability and foraging activity of

11   insectivorous birds. Pedersen et al. (2007) have also suggested a link between moose

12   browsing, invertebrate availability and breeding success in great tits (*Parus major*) in

13   the same study area.

14

15   At feeding stations the input of nutrients from animal excreta and silage residues may

16   favour some arthropod groups directly or via changes in plant biomass and chemistry

17   (Stewart 2001). The mechanism may be increased arthropod availability with the

18   increase in herbs and grasses at enriched feeding stations (Strengbom and Nordin 2008;

19   Torgersen 2008). Changed nutrient availability and responses in the vegetation may

20   lead to increase in body-size or abundance of some arthropod groups (Strengbom *et al.*

21   2005; Throop and Lerdau 2004). Another possibility is increase in dung-related

22   arthropods (Rice 2010), or arthropods in silage remains. In a parallel study (Mathisen et

23   al. unpublished) it was observed that great tits brought back larger caterpillars to the

24   nest boxes at feeding stations than at sites with high browsing pressure and low nutrient

25   input.

26

1   Granivorous bird abundance was positively correlated to birch browsing, but was lower

2   at feeding stations than at controls of similar browsing pressure. This implies that

3   negative effects of high levels of moose browsing were stronger than any positive

4   effects of nutrient input at feeding stations for granivorous birds according to scenario

5   1, although there was no net effect of feeding treatment. The granivores were dominated

6   by Eurasian siskins (*Carduelis spinus*) and crossbills (*Loxia* spp.), but also wood

7   pigeons *(Columba palumbus)* and bullfinches (*Pyrrhula pyrrhula*) belong to this group.

8   Birch seeds is an important food for siskins, and Bergström and Danell (1987) have

9   shown that birch when subject to browsing produces fewer but heavier seeds, which

10   might explain the positive correlation between granivorous bird abundance and birch

11   browsing. Siskins, crossbills and wood pigeons nest above browsing height, and were

12   probably less affected by effects of moose browsing on nesting sites, which means that

13   the positive correlation between browsing and bird abundance can also be explained by

14   nesting group. However, since the effect of feeding stations was not significant for

15   nesting groups, this suggests that the mechanism behind reduced abundance at feeding

16   stations is related to food availability.

17

18   The pied flycatcher (*Ficedula hypoleuca*) was the only bird species that had a higher

19   abundance at feeding stations than at controls. The flycatcher prefers open areas and

20   catches insects by air sallying (Sanz 1998; Waldbauer 1998), and may profit from more

21   open vegetation caused by moose browsing, or an increase in arthropod prey abundance

22   caused by the increase in dung, urine, residual silage and herbs at feeding stations. It has

23   been suggested that deer browsing may be positive for this species in British woods

24   (Fuller 2001). A parallel study of reproduction in flycatchers in the same area over

25   several years also shows a preference for nest-boxes at feeding stations, a higher

26   number of fledgings produced at feeding stations and a higher feeding frequency in bird

1   boxes at feeding stations compared to controls (K. M. Mathisen, unpublished). The

2   goldcrest (*Regulus regulus)* was the other common species that did not show the same

3   response to birch browsing as the rest of the insect-eating group. However this species

4   commonly nests high above browsing height (Cramp 1977), and might therefore be less

5   affected by moose browsing.

6

7   Supplementary feeding stations may be positive for bird diversity because of positive

8   local fertilization effects and increasing variation in moose density on a landscape scale.

9   However supplementary feeding may sustain high moose population densities leading

10   to negative effects of high browsing pressure. Effects of browsers on the ecosystem are

11   complex and dynamic, and the mechanisms are still poorly understood, and should be

12   further investigated using well designed experiments. Today many bird populations are

13   sustained within forests managed for timber production, and high moose densities and

14   intensive browsing pressure should be a concern for bird diversity conservation within

15   wildlife management and forestry practices. Birds can serve as indicator species of

16   ecosystem function, and when bird diversity changes this is a sign that the ecosystem is

17   changing. Such high moose browsing pressure as in this study is only common locally

18   where moose concentrate on winter feeding grounds. However densities of moose have

19   been extraordinary high during the last decades in Fennoscandia, as well as densities of

20   other browsers in Europe and North-America, and changes in the ecosystems caused by

21   these browsers have been documented. As dynamics are changing in boreal forest

22   systems, with global warming, changes in forestry practices and the re-establishment of

23   large predators, it is especially important to understand how large ungulate activities can

24   have cascading effects on other animals and ecosystem processes.

25

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10 landscape. Forest Ecology and Management 181: 1-12

11

12

1 **Figure legends**

2

3 Figure 1 Effects of moose browsing and supplementary feeding stations on bird species

4 richness and abundance a) Comparison of bird species richness and abundance between

5 feeding treatments (FS = feeding station, C = control 1 km from feeding station). b)

6 Bird species richness per site in relation to birch browsing (% of twigs browsed) and

7 feeding treatment. Observations for all 5 sampling events are shown, although some

8 data points are overlapping, especially for FS. The predicted model line shown is

9 standardized for effects of observer and vegetation type. c) Bird abundance per site in

10 relation to birch browsing (% of twigs browsed) and feeding treatment. Observations for

11 all 5 sampling events are shown, although some data points are overlapping, especially

12 for FS.

13

14 Figure 2 PCA of a) functional groups and b) individual species. The most significant

15 environmental variables from the RDA were added according to best fit. Categorical

16 variables are shown as triangles, continuous as thick arrows, and bird species as thin

17 arrows. CC2 = cutting class 2. Birchbr = birch browsing (% shoots browsed). FS =

18 Feeding station. Small pine = % cover of pine below 3 m. a) The variables shown in the

19 figure explained 37% of the variation in abundance of functional groups. b) Only the

20 species with more than 20 observations are shown to ease interpretation of the figure.

21 Feeding station was also added to figure b even though it was not significant, to see how

22 different species relate to feeding station. The variables shown in figure b explained

23 24% of the variation in species abundance. For full name of bird species see Appendix 1

24

25 Figure 3 Responses of functional groups to birch browsing and feeding stations. a)

26 Interaction between abundance of feeding groups of birds (seed-eater or insect-eater)

1   and the response to % birch browsing and feeding stations. FS = feeding station for

2   moose. C = control 1 km from feeding station. b) Abundance of nesting groups of birds

3   (feeding stations and controls pooled); below, at and above browsing height (0.5-3m)

4   for moose, at different degrees of birch browsing. For both a) and b) the mean numbers

5   of territorial males observed per site over 5 observation days are shown as points, the

6   regression model as a line.

7

8

1 **Tables**

2 **Table 1** Comparison of habitat between feeding stations for moose and controls (1 km from feeding

3 station): Mean and standard errors and test statistics for all habitat variables and moose activity variables.

4 P-values less than 0,05 are highlighted. * Pine browsing had very low sample size, and the variation at

5 controls = 0, so the statistical significance probably does not reflect a biological significance, as pine was

6 heavily browsed at all feeding stations and controls. Significant results are shown in bold.

Variable	Feeding station	Control	F / X^2	p
Moose variables				
Pellet group density pr m^2	2.39 ± 0.71	0.06 ± 0.01	$F_{1,20} = 25.01$	**0.0001**
Birch browsing (%)	95.08 ± 2.48	65.34 ± 8.79	$X^2_{1,20} = 8.91$	**0.0028**
Pine browsing (%) *	90.01 ± 4.24	100 ± 0	$X^2_{1,11} = 5.12$	**0.024**
Spruce browsing (%)	65.17 ± 13.05	4.6 ± 2.14	$X^2_{1,20} = 11.93$	**0.0006**
Habitat variables				
% Canopy cover above 3 m height				
Spruce	12.64 ± 7.03	12.91 ± 2.63	$F_{1,20} = 2.21$	0.15
Birch	11.45 ± 3.84	12.18 ± 3.41	$F_{1,20} = 0.05$	0.82
Rowan/ aspen/ willow/ alder	7.73 ± 7.23	2.09 ± 1.48	$X^2_{1,20} = 0.16$	0.68
Pine	7.18 ± 2.82	8.27 ± 3.21	$X^2_{1,20} = 0.06$	0.81
% Canopy cover below 3 m height				
Birch	8.18 ± 1.51	9.91 ± 3.51	$F_{1,20} = 0.21$	0.65
Spruce	4.91 ± 1.28	4.36 ± 1.18	$F_{1,20} = 0.04$	0.84
Rowan/ aspen/ willow/ alder	4.73 ± 1.62	3.91 ± 1.36	$F_{1,20} = 0.01$	0.91
Pine	0.41 ± 0.15	1.27 ± 0.5	$X^2_{1,20} = 3.33$	0.068
% Canopy cover of field- / ground layer vegetation				
Dwarf shrubs	24.27 ± 6.39	59.55 ± 7.88	$X^2_{1,20} = 7.64$	**0.0057**
Herbs	40.91 ± 10.18	14.82 ± 7.92	$X^2_{1,20} = 4.93$	**0.027**

Lichens	14.73 ± 4.54	16.82 ± 4.04	$F_{1,20} = 0.66$	0.43
Forest type				
Cutting class	2.64 ± 0.2	3 ± 0.23	$X^2_{1,20} = 1.50$	0.47
Vegetation type	3 ± 0.43	2.64 ± 0.34	$X^2_{1,20} = 1.40$	0.50
Elevation	423 ± 26.9	431 ± 36.9	$F_{1,20} = 0.03$	0.86

1

1 **Table 2** Results from selection of variables in SAS in a mixed model with poisson distributed errors for

2 species richness of singing males at feeding stations (FS) for moose and controls (C). Birchbr = birch

3 browsing. Dategr1 = 5 dates grouped in 2 groups, obsgr2 = 5 observers grouped in 3 groups. Vegpca 1

4 and 2 are axis 1 and 2 from a PCA of vegetation parameters. CC = forest cutting class. Time = time of

5 day. The minimum adequate model is shown in bold.

| Model	Variables	Parameters/ Num df	-2 log likelihood	Δ AIC$_C$
1	*FS_C dategr1 time obsgr2 birchbr vegpca2*	*10*	*31.4*	0
2	*FS_C dategr1 obsgr2 birchbr vegpca2*	*9*	*33.9*	0.1
3	***FS_C obsgr2 birchbr vegpca2***	***7***	***37.3***	**0.8**
4	FS_C dategr1 time obsgr2 birchbr cc vegpca2	13	27.9	2.1
5	FS_C obsgr2 birchbr	6	41.9	3.1
6	FS_C dategr1 time obsgr2 birchbr cc vegpca1 vegpca2	14	26.9	3.7
7	FS_C date time obs birchbr vegpca2	15	24.9	6.4
8	FS_C date time obs birchbr cc vegpca2	18	21.1	9
9	FS_C date time obs birchbr cc vegpca1 vegpca2	19	19.8	10.6
10	FS_C birchbr cc vegpca1 vegpca2	8	58.7	24.5
11	FS_C birchbr cc	6	66	27.2

6

1 **Table 3** Solution for fixed effects with poisson distributed errors for the model with the lowest AICc for

2 species richness (model 3 Table 2) and abundance of territorial male birds at feeding stations for moose

3 and controls (1 km from feeding station). For categorical variables, one of the categories is given 0 as the

4 reference level. The observers are grouped according to differences in detection of birds, in 3 groups for

5 species richness, for abundance 2 groups. Date (abundance) is grouped into two groups, as significantly

6 more birds were observed the 7. May. Important results are shown in bold.

| Effect	Levels	Estimate	Standard Error	Den DF	t Value	Pr > |t|
		Species richness				
Intercept		2.45	0.14	18	17.40	<.0001
FS_C	Control	**-0.21**	0.069	18	-3.03	**0.007**
FS_C	Feeding station	0	-	-	-	-
Observer gr2	BBKMRO	-0.19	0.060	36	-3.09	0.004
Observer gr2	CS	-0.53	0.098	36	-5.43	<.0001
Observer gr2	LH	0	-	-	-	-
Birch browsing		**-0.0050**	0.0013	18	-3.77	**0.0014**
Vegetation pca axis 2		**0.063**	0.028	18	2.22	**0.039**
		Abundance				
Intercept		2.50	0.15	19	16.19	<.0001
FS_C	Control	**-0.15**	0.075	19	-2.01	**0.058**
FS_C	Feeding station	0	-	-	-	-
Observer gr1	BBLH	0.57	0.059	21	9.58	<.0001
Observer gr1	CSKMRO	0	-	-	-	-
Date gr1	16.may-6.jun	-0.29	0.067	21	-4.31	0.0003
Date gr1	7.may	0	-	-	-	-
Birch browsing		**-0.0034**	0.0014	19	-2.39	**0.027**

7

8

9

1   **Figures**
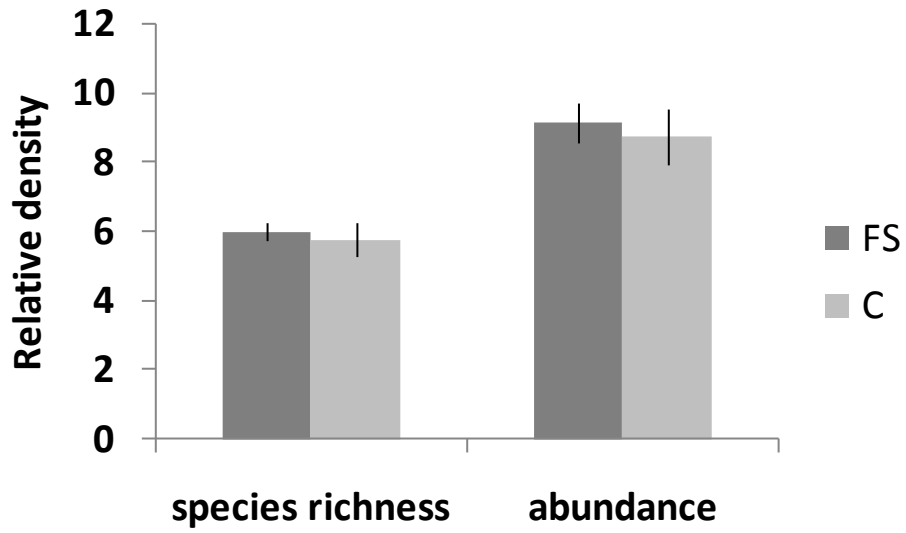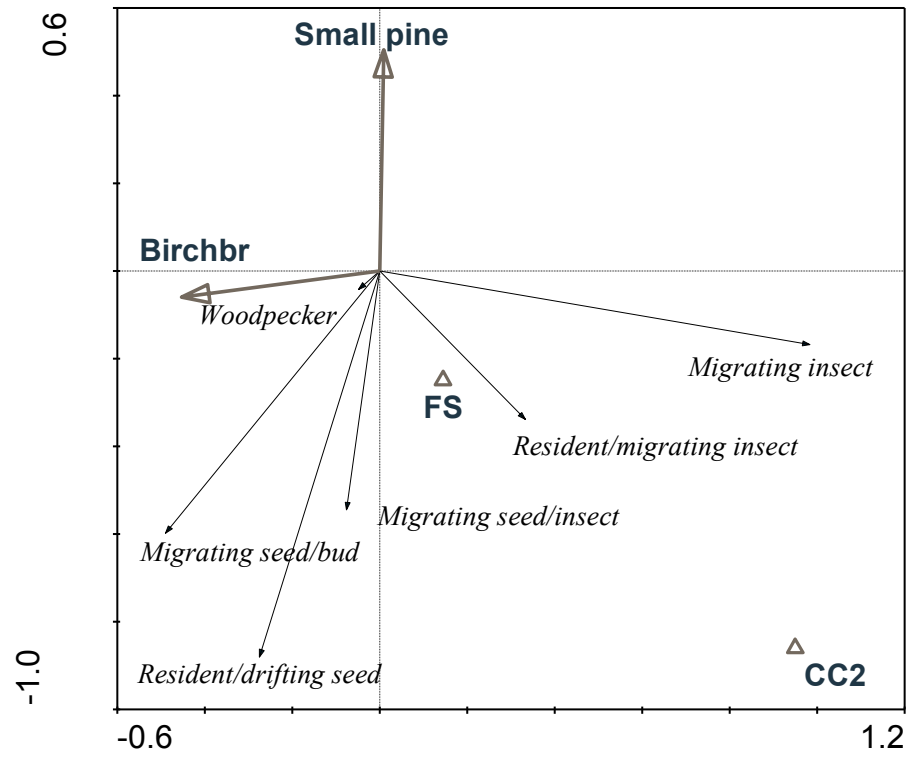

2

3   **Figure 1, a, Mathisen, K. M. 2009**
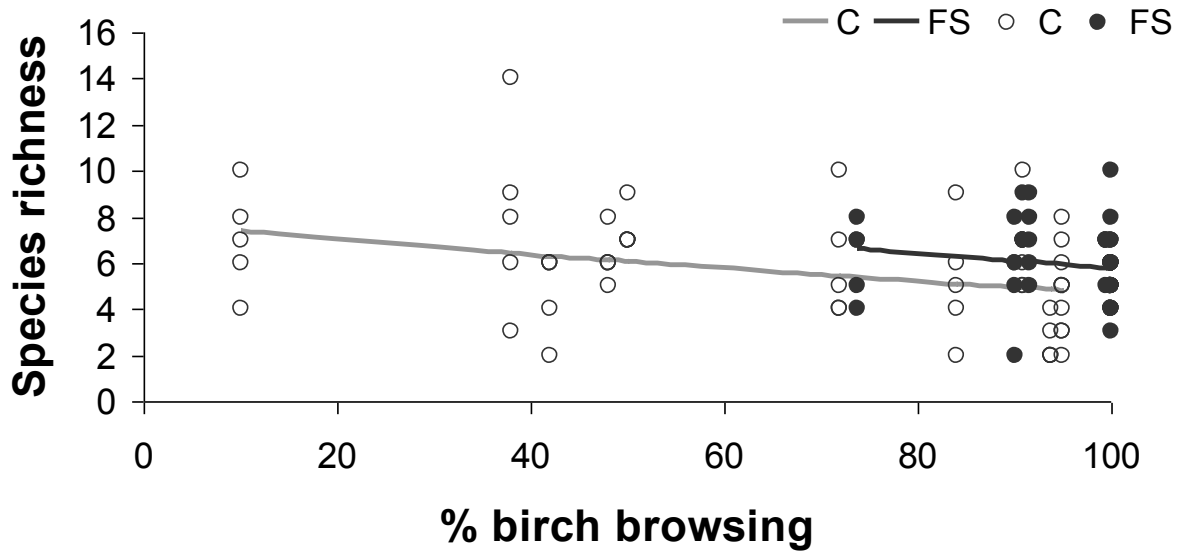
4

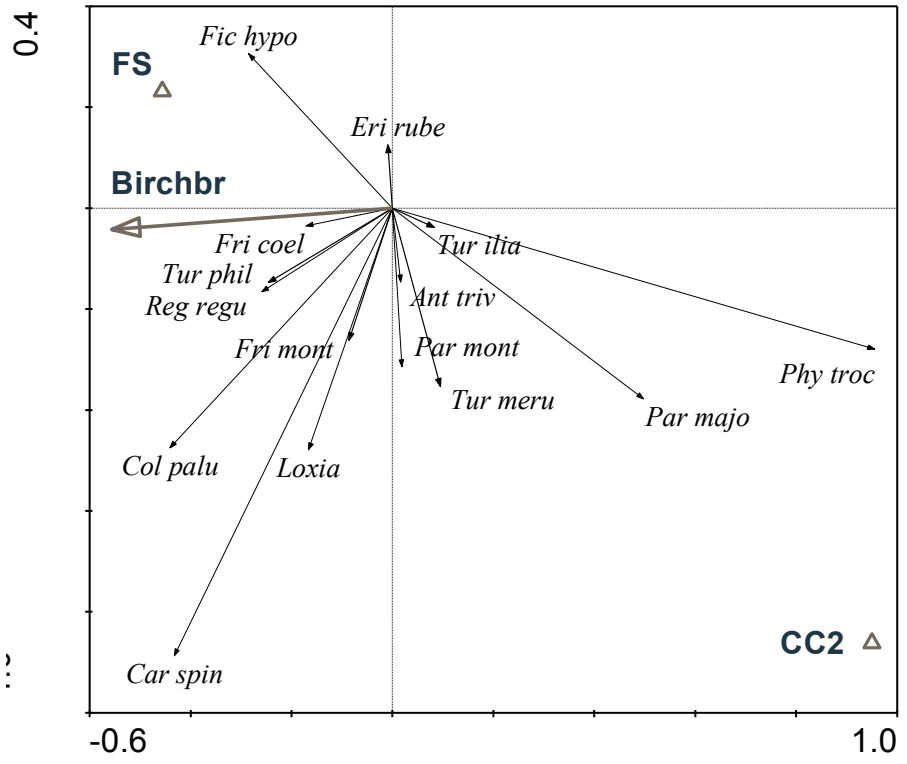5   **Figure 1b Mathisen, K. M. 2009**
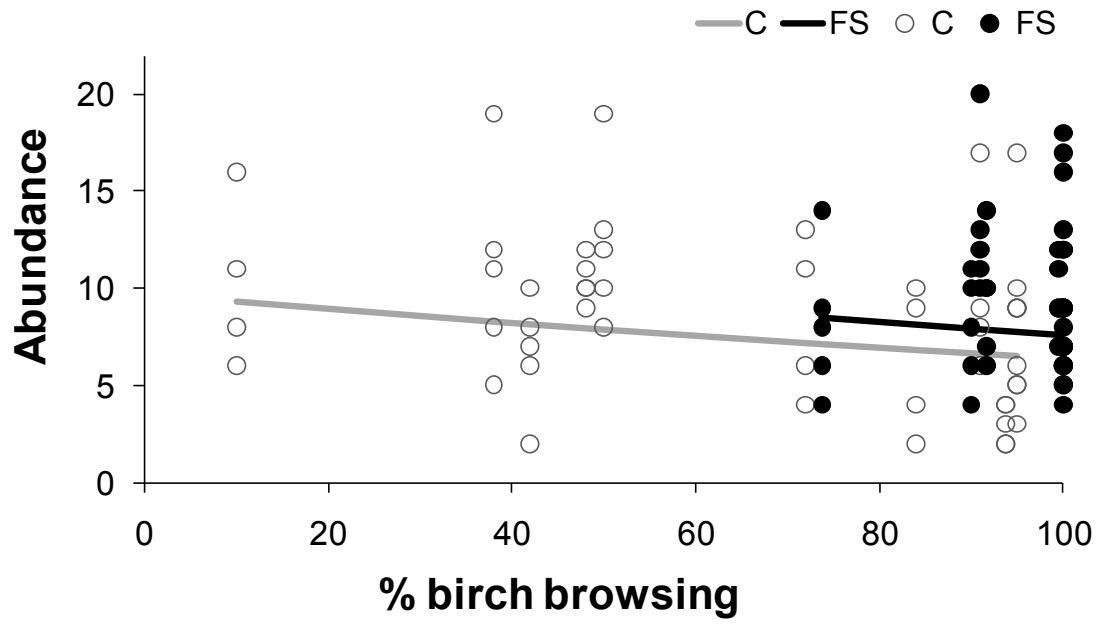
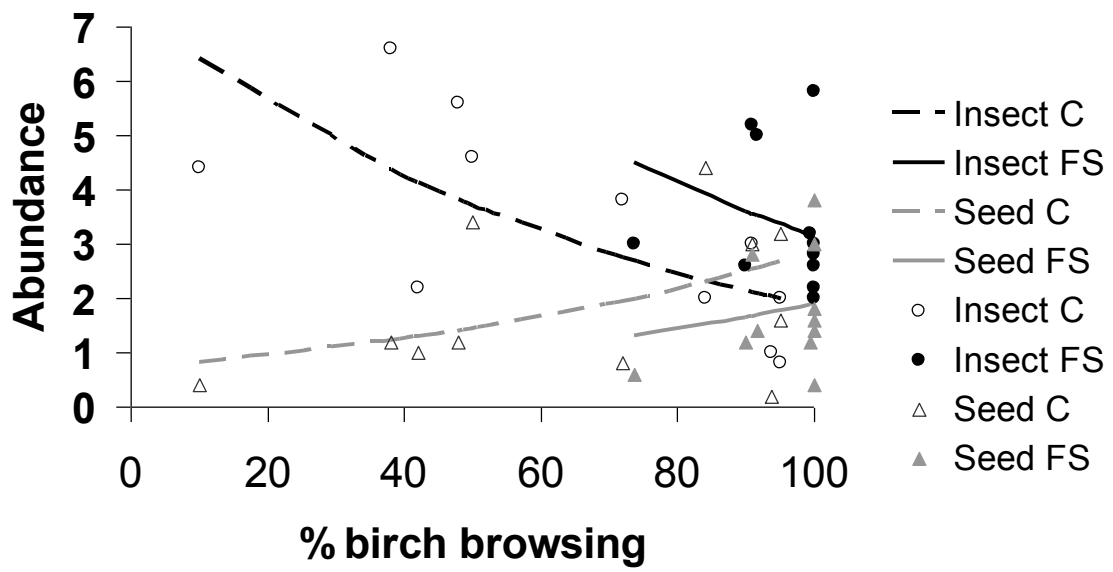Figure 1c Mathisen, K. M. 2009

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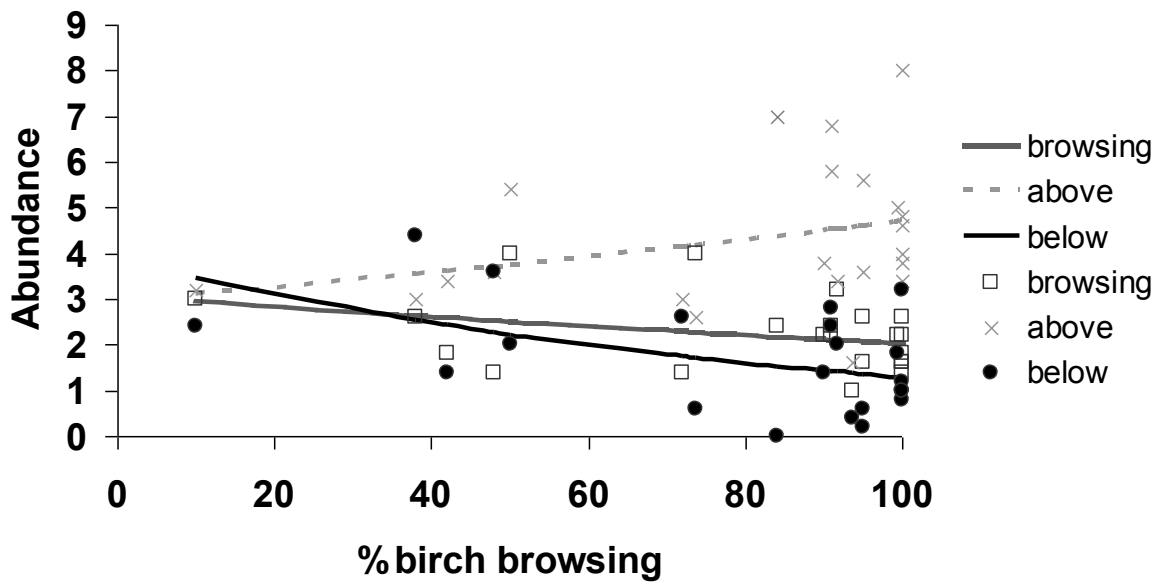
Figure 2a Mathisen, K. M. 2009

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Figure 2b Mathisen, K. M. 2009

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2 **Figure 3a Mathisen, K. M. 2009**

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4 Figure 3b Mathisen, K. M. 2009

Appendix 1 : Bird species observations and functional group classification.

Total number of observations of bird species observed over 5 observation days in point counts of singing males at 11 feeding stations (FS) for moose and 11 controls (C) 1 km from feeding station in Stor-Elvdal municipality, Hedmark County, Norway. Species are grouped into functional groups after migration strategy and diet in the nesting period. Species are defined as nesting under, at or over browsing (br) height (0.5-3 m) for moose.

Migratory strategy	Diet	Nest height	English name	Latin name	Mean FS ± SE			Mean C ± SE			Total obs
Migrating	Insects	under br	Willow warbler	*Phylloscopus trochilus*	0.89	±	0.36	1.27	±	0.36	119
Migrating	Insects	under br	Tree pipit	*Anthus trivialis*	0.58	±	0.11	0.36	±	0.11	52
Migrating	Insects	at br	Pied flycatcher	*Ficedula hypoleuca*	0.45	±	0.07	0.13	±	0.07	32
Migrating	Insects	at br	Dunnock	*Prunella modularis*	0.09	±	0.06	0.13	±	0.06	12
Migrating	Insects	other	Cuckoo	*Cuculus canorus*	0.09	±	0.05	0.07	±	0.05	9
Migrating	Insects	under br	Chiffchaff	*Phylloscopus collybita*	0.02	±	0.06	0.09	±	0.06	6
Migrating	Insects	other	Wren	*Troglodytes troglodytes*	0.07	±	0.02	0.04	±	0.02	6
Migrating	Insects	at br	Garden warbler	*Sylvia borin*	0.02	±	0.04	0.09	±	0.04	6
Migrating	Insects	at br	Lesser whitethroat	*Sylvia curruca*	0.07	±	0.02	0.02	±	0.02	5
Migrating	Insects	at br	Blackcap	*Sylvia atricapilla*	0.02	±	0.04	0.04	±	0.04	3
Migrating	Insects	under br	Whinchat	*Saxicola rubetra*	0.02	±	0.00	0.00	±	0.00	1
Migrating	Insects	at br	Common redstart	*Phoenicurus phoenicurus*	0.02	±	0.00	0.00	±	0.00	1
Migrating	Seeds & buds	over br	Common wood pigeon	*Columba palumbus*	0.24	±	0.09	0.29	±	0.09	29

Migrating	Seeds & insects	over br	Chaffinch	*Fringilla coelebs*	2.09	±	0.09	1.76	±	0.09	212
Migrating	Seeds & insects	at br	Robin	*Erithacus rubecula*	0.47	±	0.10	0.56	±	0.10	57
Migrating	Seeds & insects	at br	Song thrush	*Turdus philomelos*	0.56	±	0.12	0.47	±	0.12	57
Migrating	Seeds & insects	over br	Brambling	*Fringilla montifringilla*	0.36	±	0.08	0.25	±	0.08	34
Migrating	Seeds & insects	at br	Redwing	*Turdus iliacus*	0.22	±	0.08	0.24	±	0.08	25
Migrating	Seeds & insects	at br	Blackbird	*Turdus merula*	0.16	±	0.05	0.22	±	0.05	21
Migrating	Seeds & insects	over br	Mistle thrush	*Turdus viscivorus*	0.02	±	0.00	0.00	±	0.00	1
Resident	Woodpecker	over br	Great spotted woodpecker	*Dendrocopos major*	0.04	±	0.04	0.05	±	0.04	5
Resident	Woodpecker	over br	Black woodpecker	*Dryocopus martius*	0.05	±	0.02	0.04	±	0.02	5
Resident/ drifting	Seeds	over br	Eurasian siskin	*Carduelis spinus*	1.29	±	0.29	1.33	±	0.29	144
Resident/ drifting	Seeds	over br	Crossbill	*Loxia* spp.	0.20	±	0.12	0.18	±	0.12	21
Resident/ drifting	Seeds	at br	Common bullfinch	*Pyrrhula pyrrhula*	0.02	±	0.04	0.05	±	0.04	4
Resident/ migrating	Insects	other	Great tit	*Parus major*	0.47	±	0.14	0.47	±	0.14	52
Resident/ migrating	Insects	over br	Goldcrest	*Regulus regulus*	0.27	±	0.08	0.20	±	0.08	26
Resident/ migrating	Insects	at br	Willow tit	*Parus montanus*	0.15	±	0.10	0.24	±	0.10	21
Resident/ migrating	Insects	other	Coal tit	*Parus ater*	0.09	±	0.02	0.04	±	0.02	7
Resident/ migrating	Insects	under br	Yellowhammer	*Emberiza citrinella*	0.02	±	0.05	0.09	±	0.05	6
Resident/ migrating	Insects	at br	Crested tit	*Parus cristatus*	0.04	±	0.00	0.00	±	0.00	2
Resident/ migrating	Insects	other	Blue tit	*Parus caeruleus*	0.02	±	0.00	0.00	±	0.00	1