Title: Contrasting responses of two passerine bird species to moose browsing

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Abstract

Large herbivores may modify the ecosystem in a way that affects habitat quality and resource availability for other fauna. The increase in wild ungulate abundance in many areas may therefore lead to ecosystem changes, affecting distribution and reproduction of other species. Moose (*Alces alces*) in Scandinavia is a good example of a herbivore that has recently increased in abundance, and has the potential to affect the ecosystem. In this study we investigated how different levels of moose winter activity around supplementary feeding stations for moose affect reproduction in two insectivorous passerines: great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). The two bird species showed contrasting responses to high moose activity at feeding stations. Great tits avoided habitats with high moose activity, where fledging success and feeding frequency was lower than at low moose activity habitats. Flycatchers nested more often at high moose activity habitats where fledging weight and feeding frequency were higher than at low moose activity habitats. Filming of nest boxes with great tits showed an increase in adult Lepidoptera in the diet at supplementary feeding stations for moose, and a smaller size of caterpillar prey at intermediate moose activity. The results support the hypothesis that herbivores may affect insectivorous passerines through changed arthropod food availability.

Keywords*: herbivory, cascading effects, boreal forest, Alces alces, Parus major, Ficedula hypoleuca*

Introduction

Large herbivores can be considered as drivers of ecosystem processes, as they modify their environment by eating, defecating, trampling, wallowing, and other activities (Hobbs 1996; Persson 2003). They have the potential to affect directly and indirectly plant biomass and reproduction, vegetation structure and plant species composition, as well as ecosystem processes such as vegetation succession and soil nutrient cycling (Danell et al. 2003; Davidson 1993; Olff and Ritchie 1998; Pastor and Cohen 1997). By modifying the ecosystem, herbivores may affect habitat quality and resource availability for other fauna living in the same community; however documentation of such cascading effects is scarce (Suominen and Danell 2006). In Europe, North-America and Japan, the populations of cervids have increased through the last decades, and in some areas to extremely high densities (Côté et al. 2004; McShea et al. 1997). This increase in cervids has caused some concern for how ecosystem processes and biodiversity may be affected (Fuller and Gill 2001; Garrott et al. 1993), and research on how cervids may affect other fauna is needed. The moose (*Alces alces*) in Fennoscandia is a good example of a cervid that recently has experienced a large population increase (Cederlund and Bergström 1996). The moose is the largest native herbivore in Fennoscandia, and as a selective browser, it has the potential to influence the boreal forest ecosystem strongly (Pastor and Naiman 1992; Persson et al. 2000). Supplementary feeding is a common management tool to increase or sustain population sizes of game species such as moose, but also to mitigate problems with high ungulate densities e.g. herbivory damage to commercial tree species and traffic accidents (Andreassen et al. 2005; Luccarini et al. 2006; Putman and Staines 2004). However, how supplementary feeding may affect ecosystem processes, is not known.

Cervid browsing may have indirect effects on arthropod diversity and abundance, and both positive and negative responses have been reported (Allombert et al. 2005b; Danell and Huss-Danell 1985; Riipi et al. 2005; Suominen et al. 2008). This may in turn affect the many species, including mammals and birds, which live on an arthropod diet. Effects of cervid browsing on bird diversity and abundance have also been documented (Allombert et al. 2005a; Berger et al. 2001; Fuller 2001; Mathisen and Skarpe 2011; McShea and Rappole 2000). These studies are in general based on presence or absence of birds in a certain area, and give little insight into the mechanisms that link cervid browsing with bird abundance. However, Bailey and Whitham (2003) showed experimentally that elk (*Cervus elaphus*) browsing affects the distribution of arthropods and foraging patterns in insectivorous birds, and other studies suggest a link between herbivory, arthropod abundance and bird reproduction (Baines 1996; Evans et al. 2005; Pedersen et al. 2007). Cervid browsing may potentially affect birds in many ways, by changing vegetation structure, tree species composition, food availability, predation pressure and nest losses through trampling (Fuller 2001).

In this study, we investigated how different levels of moose activity affect reproduction in two insectivorous passerines, and if differences in reproduction can be linked to arthropod food availability. We have used nest boxes placed along a gradient in moose activity around moose winter supplementary feeding stations to investigate the effects of moose on habitat selection, reproduction and nestling feeding activity of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Supplementary feeding stations represent gradients in moose activity in the winter time, with high browsing pressure and high levels of moose dung and urine close to the feeding stations, and decreasing browsing pressure and dung density with increasing

distance from feeding stations (Gundersen et al. 2004; van Beest et al. 2010). Although effects of browsing on arthropod abundance vary with herbivore density, habitat productivity and arthropod group (Suominen et al. 2008), high intensity browsing generally has negative effects (Stewart 2001). We therefore hypothesize that high moose browsing intensity will have negative effects on bird reproduction due to reduced arthropod food availability. A previous study has shown negative effects of high moose activity on great tit reproduction in the same area (Pedersen et al. 2007). The present study extends the previous study by investigating further the mechanisms of how moose browsing affects passerine birds, including habitat selection, feeding activity, diet composition and the response of another insectivorous passerine.

Methods

Study area

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 zones (Moen et al. 1999). The area is dominated by the Glomma river valley running northwest - southeast, with side valleys and adjacent 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 °C (May-September) and mean winter temperature of -5.8 °C (October – April). During the same 30-year period, the mean annual precipitation was 628 mm and the mean snow depth 39 cm (NMI 2008).

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 winter. Since 1990 local landowners have carried out organised supplementary winter feeding of moose with grass silage (Gundersen et al. 2004), to reduce traffic accidents and browsing damage to young pine stands. The amount of food supplied has more than doubled during the study period, from 800 tonnes in 2003-2004 to 1700 tonnes in 2007-2008 (Stor-Elvdal landowner association, unpubl. data). The feeding stations are mainly placed along forest roads in the side-valleys (Figure 1). The overall moose density in the municipality varies between 1.1-3.4 moose per km^2 (Gundersen et al. 2004; Storaas et al. 2005), but in winter the effective moose density may be many times higher in the vicinity of feeding stations. High moose densities at feeding stations may be comparable to concentrations of large herbivores around waterholes or salt-licks (Brits et al. 2002; Miller and Litvaitis 1992), or areas with extremely high densities due to population increase (Côté et al. 2004; Garrott et al. 1993; McShea et al. 1997).

Field procedures

Study design

Feeding stations for moose represent points in the landscape with high browsing pressure and nutrient input (though silage, dung and urine) and both effects decrease with distance to feeding stations (van Beest et al. 2010). In this study, the gradient in moose activity from a total of 44 feeding stations was used to analyse the effect of moose on reproduction in passerine birds. This can be considered a "quasi-experimental" design (Shadish et al. 2002) where moose activity in the area is manipulated by the presence of feeding stations. We selected feeding stations that were placed in mixed conifer-deciduous forest. Nest boxes with a hole of diameter 32 mm were placed at 1.5m height on trees in a gradient from 0 m up to 1700 m from feeding stations for moose and surveyed in the period 2004 -2008 (Figure 1). The nest boxes were grouped in five areas: four side valleys and the main valley area. The sample size varied among years because boxes were added in 2006 and 2007 to increase sample size, and removed in 2008 from feeding stations that were no longer in use (number of nest boxes pr year: 2004-2005: 38, 2006: 83, 2007: 130, and 2008: 65). The study design from 2004-2005 was earlier described in Pedersen et al. (2007).

Nutrient input and browsing intensity at feeding stations operate on different spatial scales. Nutrient input through dung and urine is intense at a local scale (up to 50 m from feeding station) and then decreases rapidly, caused by high processing of supplementary food at feeding stations. Browsing pressure on birch is intense up to 500 m and decreases gradually with distance from feeding station but at a larger scale than dung density. Pine browsing pressure is high up to 1 km from feeding stations, whilst spruce browsing occurs almost only up to ~50 m from feeding stations (Gundersen et al. 2004; Pedersen et al. 2007; van Beest et al. 2010).

To analyse the effect of distance to feeding stations on bird reproduction, we grouped nest-boxes into 3 categories with similar sample sizes (bird box years: 132/121/101); at feeding station (FS: < 50 m from feeding station), at intermediate distance (INT: 50-500 m from feeding station) and far away from feeding station (FAR: 501-1700 m from feeding station) (Figure 1). When nest boxes were located between feeding stations, the distance to the nearest feeding stations was used. This classification allows us to separate to some degree the effects of nutrient input at feeding stations and browsing pressure. The three categories therefore represent different levels of moose activity:
- FS : high nutrient input, high browsing pressure on all tree species
- INT: low nutrient input, high browsing pressure on most tree species
- FAR : low nutrient input, low to intermediate browsing pressure

To check that this division into categories reflected moose activity, we recorded moose pellet group density and moose browsing pressure in spring in 2004, 2006 and 2007, when new nest boxes were added. Moose pellet groups and moose browsing pressure were recorded in 5 circular plots of 50 m^2, one plot under the nest box and four plots 20 m from the observation point in each of the directions north, south, west and east. We estimated moose browsing as number of shoots browsed as a proportion of number of shoots available within browsing height (0.5 – 3 m). In 2004 the proportion of birch, pine and spruce shoots browsed was grouped into four classes quantified on a subjective observational scale: 1) No browsing, 2) Less than 1/3 of the shoots browsed, 3) Between 1/3 and 2/3 of the shoots browsed, and 4) More than 2/3 of the shoots browsed (see Pedersen et al. (2007)), while in 2006 and 2007 moose browsing pressure was estimated as % shoots browsed in the same plots. In order to

compare data across all years, we converted the browsing classes from 2004 into % twigs browsed, and used the mean for each class (Solbraa 2002). The analysis of these data are presented in Online Resource 1, and show that our classification of feeding stations, intermediate and controls is consistent with a gradient in moose dung density and browsing pressure as described above. However, dung density and browsing pressure at intermediate and far sites increased through the study period, as found by van Beest et al. (2010). Moose pellet group density was an order of magnitude higher at feeding stations than intermediate sites and far sites (Online Resource 1).

Habitat variables were measured in 2007 for all nest boxes used in this study to control for possible biases in the sampling design. We surveyed vegetation variables in July in a circular plot of 10 m radius around the nest box as follows: canopy cover of trees with total height below and above browsing height (3 m) for birch, pine, spruce and other species (aspen, rowan, *Salix* spp. and alder were grouped because of their low densities) and cover of the categories herbs (forbs and graminoids), lichens and dwarf shrubs. Canopy cover (%) of trees and field layer was estimated visually. The sites were categorised by forest vegetation type (Moen et al. 1999): lichen forest, cowberry-bilberry forest, heather bog-bilberry pine, bilberry forest and small-fern forest. The age of the forest was categorised according to Norwegian forestry age classes: 1 = clear cut, 2 = trees up to 8 m height, 3 = trees higher than 8 m but not mature, 4 = mature forest for cutting. The different distance categories (FS/INT/FAR) showed no differences in elevation, forest age class or vegetation type (Online Resource 2).

Cover of birch above browsing height was higher at intermediate distances than at feeding stations and far from feeding stations, and cover of pine at browsing height was lower at feeding stations than intermediate and far distance (Online Resource 2). Cover of herbs was higher at feeding stations than at intermediate and far distances, and cover of dwarf-shrubs was lower at feeding stations than at intermediate and far distances (Online Resource 2). Moose browsing at feeding stations has probably caused a reduction in cover of small pine trees and dwarf shrubs, whilst herb cover has most likely increased due to increased light availability and fertilisation at feeding stations (Mathisen et al. 2010; Torgersen 2008).

Habitat choice and reproductive success

Each year the nest boxes were surveyed weekly from April – July. Around hatching date the boxes were checked every day, to determine the date of hatching. The species nesting, laying date of the first egg, and number of eggs, hatchlings and fledglings produced were recorded. Nestlings were weighed individually at day 13 for pied flycatchers and day 15 for great tits with a Pesola spring balance during 2004-2007. The number of fledglings alive at the day of weighing was used as a measure of number of fledglings produced. Only first clutches were included in the analysis. Nests that failed to hatch (8 nests in total) were not included in the analysis, as we wanted to focus on the effect of moose on food availability during the nestling period. Predation of chicks occurred in only 4 boxes, and these were also excluded from the analysis.

Feeding activity

In 2007 nest boxes were surveyed for feeding activity using activity loggers. Because of the limitation of number of loggers available, we chose to focus on nest boxes at feeding stations and far distance (1 km from feeding stations), to cover the greatest possible variation in

moose activity (sample size: great tits: 7 boxes at FS, 7 boxes at FAR, flycatchers: 4 boxes at FS, 7 boxes at FAR). The activity loggers covered the nestling period, from the first day of hatching to the last day of fledging of chicks. The logger was placed on the nest box, with a light beam and a sensor across the opening hole, and each time the beam was broken, date and time of day were registered. The activity loggers were produced by Lamberg Bio Marin, including a Hobo Event logger using the software BoxCar (1997). The number of logger events was divided by 2 to reflect the number of feeding trips per day, as at each feeding event, the logger registered entry and exit of the box. To ensure that the number of logged events was proportional to the number of feeding trips, we observed the nest opening with binoculars several times during the nesting period, and compared the number of events seen with the numbers registered by the logger. There was a good agreement between the approaches (Pearson's correlation, r = 0.80, dF = 15, p < 0.001), suggesting that the logger events reflected feeding trips to the nest box.

Diet composition

Nest boxes for great tits (only) were also filmed in 2007 (Sample sizes by category: FS: 12, INT: 6, FAR; 18) with digital video cameras following the protocol in Currie et al. (1996), to investigate diet composition and size of prey items brought to the nest box. Because of limited resources for field work, we focused on the bird species in which we had observed changes in reproduction with moose activity at that time (Pedersen et al. 2007), to investigate the mechanisms further. Filming was carried out on the day when the chicks were 9-10 days old, and at the time around mid-day when feeding activity was highest. Each nest box was recorded for 80 minutes. The box was rigged the day before filming, so the birds could get habituated to the filming equipment. The videos were subsequently scanned for all feeding events, and when a food item was clearly visible it was identified and measured. The food items were identified to group (Lepidoptera, Hymenoptera, Coleoptera, Aranea, and Diptera) and to development stage (larvae, pupae, and imago). The length and the width of the food item, excluding legs and wings, were measured relative to the beak length of the bird. The volume of each item was then estimated by assuming a cylindrical form ($V = \pi r^2 h$), similar to the methods in Slagsvold and Wiebe (2007).

Statistical analysis

All analyses were performed using the R software version 2.10 (R Development Core Team 2009). We used general and generalized linear mixed models depending on the response variable distribution for all analyses of effects of distance to feeding stations on different response variables. As nest box occupation varied among years, we tested for an interaction with year or an additive effect of year for all response variables. Most variables seemed to vary randomly among years, but there was a continuous trend in nest box occupation with time. Therefore year was added as a categorical variable to all analyses of all response variables, except nest box occupation where it was added as a continuous variable. If year did not affect the results, it was not included in the tables and figures.

The variables included in the models were distance to feeding station (FS/INT/FAR or only FS/FAR for logger activity) and year and the interaction between them as fixed effects, and nest box ID nested within area as random intercept terms. For chick weight, year was added as a random intercept nested within box ID and area, to account for dependency among chicks within the same box. Environmental variables and diet composition were only measured in

2007, and were therefore analysed with linear or generalized linear models. To investigate possible differences between the three distance categories in forest age classes and vegetation types a two-way contingency table and a chi-square test was used. For the analysis of feeding frequency, day since hatching and the interaction between day and distance to feeding stations was included to account for the increase in feeding frequency with nestling age. Day was included as a 2-degree polynomial, as this gave a lower AIC (Burnham and Anderson 2002) than a linear term alone. Number of hatchlings was also included in this analysis as a fixed effect, as feeding frequencies may differ among nests with different number of chicks.

Chick weights and volume of prey were analysed with a normal error distribution and an identity link function. Vegetation cover was arcsine square-transformed, and analysed with a normal error distribution. Number of fledglings produced, moose pellets, feeding frequency and prey numbers were analysed with a Poisson error distribution and a log-link function. Because of overdispersion in the analysis of moose pellets, prey numbers and feeding frequency, we corrected the standard error by using a quasi-Poisson GLM where the variance is given by $\varphi*\mu$, where μ is the mean and φ is the dispersion parameter (Zuur et al. 2009). Browsing pressure (shoots browsed/available), proportion of prey groups in the diet (group items/total items) and nest box occupation (0/1) were analysed with a binomial error distribution and a logit-link function. A quasi-binomial error correction was used for prey groups that showed overdispersion. For flycatchers that generally arrive at the breeding ground after great tits, their box choice was restricted to the subsample of boxes available after great tits had started breeding. Nest box availability for flycatchers was therefore calculated by removing the boxes already selected by great tits.

Results

Habitat selection and reproduction

Over this 5 year study, from a total of 354 nest box years available, 243 boxes produced fledgings of the studied species, 125 boxes for the great tit, and 118 for the pied flycatcher. Habitat preferences changed with time for both species, and they showed opposite patterns in preference/avoidance of feeding stations. Both species showed an interaction between distance to feeding station bands and year (Great tits: $\chi^2_2 = 16.94$, p <.001, Flycatchers: $\chi^2_2 = 4.77$. p= 0.092). Great tits showed a decrease in preference for boxes at feeding stations and an increase in preference for boxes far from feeding stations during the study period (Figure 2). The flycatcher's occupancy at feeding stations increased during the study period, with almost no nests at feeding stations the two first years and more nests at feeding stations than far distance the last 2 years. Overall occupation rate by flycatchers increased with time in all categories, whilst great tit occupation rate was rather constant (Figure 2). On average 21 % ($\pm$ 6 SE) of the boxes were empty each year.

Great tits produced on average 7.52 ($\pm$1.05) fledgings at far distance from feeding stations, and 1.15 ($\pm$1.09) fledglings less at feeding stations than at far distance, and 1.02 ($\pm$1.09) fledglings less at intermediate sites than at far distance (Table 1). Pied flycatchers produced on average 5.1 ($\pm$1.1) fledgings at far distance, and 1.2 ($\pm$1.1) more fledgings at feeding stations, and 1.1 ($\pm$1.1) fledgings more at intermediate sites than far (Table 1). However, the difference between the three distances was not significant for flycatchers (Table 1). Great tit fledging production showed a larger overall variance (σ^2=4.6) than fledging production in pied flycatchers (σ^2=2.4).

There was no effect of distance to feeding station on weight of great tit chicks, but flycatcher chicks were heavier at feeding stations (+0.5 g) and intermediate distances (+0.7g) than in boxes far from feeding stations (Table 2). For flycatchers there was no effect of the interaction between year and distance to FS ($F_{2,20} = 0.63$, $p = 0.543$), or year alone ($F_{1,20} = 0.05$, $p = 0.828$) on chick weight. For great tits the interaction between year and distance to FS was not significant ($F_{2,15} = 1.41$, $p = 0.275$), but weight varied among years, and was lowest in 2004 (Table 2).

Feeding activity

The number of feeding trips per day in 2007 made by great tits and pied flycatchers also showed opposite responses to feeding stations (Table 3, Figure 3). In general, flycatchers had higher activity at feeding stations than at far distance from feeding station during most of the nestling period, whilst great tits had higher activity at far distance from feeding stations towards the end of the nestling period (from day 10 and onwards, Figure 3). Both species increased the activity greatly during the nestling period, from the day of hatching to the day of fledging. The variation around day 9-10 for great tits is probably due to disturbance in setting up the filming equipment (Figure 3). The number of feeding trips was positively correlated with number of fledgings for flycatchers, but this correlation was not significant for great tits (Table 3).

Diet composition

We recorded a total of 1070 items delivered to nest boxes by great tits belonging to the groups Lepidoptera (31%), Hymenoptera (17%), Coleoptera (15%), Aranea (10%), Diptera (3%) and unidentified (24%). Most of the objects were insect larvae (59%), the remaining were imago (32%), pupae (1%) and unidentified (8%). Lepidoptera larvae were the most frequent food item, making up 30-38% of the diet at feeding stations, intermediate and far distance. Proportion of imagos of Lepidoptera in the diet, was higher at feeding stations compared to intermediate and far distance (Table 4). In general, the proportion of imagos in the diet was higher at feeding stations, but not statistically significant (Table 4). Diptera larvae occurred only in the diet at far distance (Table 4).

Both total number of prey and prey volume recorded was lower at intermediate distance than at feeding stations and far from feeding stations, and although the overall effect of distance categories was not statistically significant (Table 4), number of prey tended to be lower at intermediate sites than at far sites (comparison INT – FAR: p=0.063). These results may be affected by the low sample size of nest boxes (n=6) at intermediate distance. Because of this low sample size, distance to feeding stations was also analysed as a continuous variable for volume of prey in intermediate and far distance nest boxes. Volume of Lepidoptera larva and volume of all insect groups combined, showed an increase with increasing distance to feeding stations, for intermediate and far distance nest boxes (Lepidoptera larva: $F_{1,18} = 7.22$, $p = 0.015$, all insect groups: $F_{1,22} = 7.38$, $p = 0.013$).

Discussion

Great tits and pied flycatchers showed contrasting responses to distance to moose feeding stations, both in nest box selection, breeding success, fledgling weight and feeding activity.

This indicates that the two bird species respond differently to high levels of moose activity, and that there is a link between herbivore disturbance and bird habitat choice, food availability and fledgling production. The responses to feeding stations increased with time, parallel with an increase in moose use of feeding stations. We suggest that the mechanism behind this pattern is that moose activity changed arthropod food availability in different ways for the two bird species.

Great tits increasingly preferred nest boxes far away from feeding stations as moose dung density and browsing pressure at feeding stations increased during the study period. A study of browsing intensity around supplementary feeding stations for moose over the period 1998-2008 in the same area as the current study, showed increased use by moose of feeding stations with time, and browse depletion in 2008 of the natural vegetation within 200 m from feeding stations (van Beest et al. 2010). This indicates that higher moose activity and increasing cumulative effects of moose browsing on the vegetation close to feeding stations has over time made the habitat less suitable for great tits. Possible mechanisms behind the observed pattern of great tit habitat choice may be changed habitat structure and tree species composition, leading to reduced availability of foraging sites or increased risk for predation. Common nightingales (*Luscinia megarhynchos*) have been shown to prefer unbrowsed exclosures as breeding territory to areas browsed by multiple deer species in Britain, probably because of reduced density of understorey vegetation and availability of feeding sites outside of exclosures (Holt et al. 2010). On the other hand, mixed livestock grazing at low intensities may increase habitat suitability for species such as the meadow pipit (*Anthus pratensis*) by increasing habitat heterogeneity (Evans et al. 2006). As fledgling production was higher at greater distance from feeding stations, habitat choice may be linked to reproductive success, or great tits may be able to assess food availability from habitat cues (Hilden 1965). Great tits generally prefer to nest in deciduous forest (Cramp 1977) and may avoid feeding stations because of reduced birch biomass or changed tree structure caused by moose browsing (Persson et al. 2007; Persson et al. 2005). Moose browsing creates a more open habitat (Persson et al. 2005), which may lead to increased risk of predation (Martin and Joron 2003).

The flycatcher's choice of nesting sites was limited to boxes that were left after tits had made their choice, and although they seemed to avoid feeding stations in the first two years of the study period, in the last years they had a higher occupancy rate at feeding stations than at boxes far from feeding stations. This pattern may be an effect of competition with great tits for nest boxes (Slagsvold 1975), since great tits showed the opposite pattern. However, flycatchers had a higher fledging weight and higher feeding activity at feeding stations, which may be linked to nest box selection (Doligez et al. 2004). This suggests a preference for boxes at feeding stations. Also other studies have shown than flycatchers prefer to nest and forage in open areas (Cramp 1977), and areas with high browsing pressure from deer or sheep grazing may open up the vegetation and favour the flycatcher (Fuller and Gill 2001). The switch towards boxes at feeding stations may also be caused by a general population increase caused by increased availability of nest boxes (Hilden 1965), as box occupation increased in all distances.

Feeding stations had a negative effect on number of great tit fledglings produced. Herbivory in the tree canopy may lead to less cover and higher vulnerability to predation (Fuller 2001; Suominen and Danell 2006). Direct predation on chicks was rare in this study, probably because the nest box provided good protection. However adult predation may have been affected by moose browsing, with subsequent negative effects on nestling survival close to feeding stations. Moose browsing may affect food availability and great tit reproduction

through reduced birch biomass (Pedersen et al. 2007). Other possible mechanisms affecting nestling survival may be changed microclimate and parasite burden. Ectoparasites in this study were rarely observed and showed no relationship with moose activity (K. M. Mathisen, unpublished data). Flycatchers showed higher fledgling weights at high moose densities, but great tits showed only in-between year variation in fledgling weight, although the direction of the trend follows fledgling production. Great tits may adjust clutch size to habitat quality (Dhondt et al. 1992), which may explain why we saw little effect on fledgling weights. Great tits had a larger variance in fledgling production than flycatchers, which may further indicate different life-history strategies in the two species. Therefore great tits may respond to high moose browsing by reducing number of fledgings, whilst flycatchers respond by increasing weight of fledgings. Great tits also only showed negative effects of high moose activity on feeding frequency late in the breeding period, whilst for flycatchers the difference was more consistent with time, which may explain the difference in chick weight response in the two species.

The sites with highest feeding rates corresponded to the sites with the highest fledgling production in great tits, and the highest fledgling weight in flycatchers. This supports the hypothesis that food availability may be a mechanism behind differences in reproductive success between high and low moose activity sites in both bird species (Pedersen et al. 2007). Feeding rates were higher at high browsing pressure and high nutrient input than at low browsing pressure and low nutrient input for flycatchers. Great tits showed the opposite pattern, with reduced provisioning rates at feeding stations at the end of the breeding period. Feeding activity increased in general through the nestling period, hence the reduced feeding frequency at feeding stations for great tits coincided with the period of highest demand for food. Higher feeding frequencies may not be a good indicator of higher food availability, as smaller prey items may be compensated for with higher feeding frequencies, and load size may vary (Nour et al. 1998). However we know from filming that prey item size was similar between boxes at feeding stations and far away, and that great tits are generally single-loaders (Naef-Daenzer et al. 2000) indicating that feeding frequency in this case reflected food availability. We therefore suggest that lower fledging success in the great tit at feeding stations was due to reduced food availability because of high moose browsing pressure (Pedersen et al. 2007).

The opposite effects on the two bird species may be caused by different diet or foraging strategies. Great tits are more dependent on caterpillars (Nour et al. 1998), and may be more susceptible to reduced biomass of deciduous trees caused by browsing (Persson et al. 2007; Persson et al. 2005). Flycatchers are more flexible and may also eat spiders, dipterans, coleopterans, hymenopterans and imagos to a greater extent (Sanz 1998), and may have higher success in heavily browsed areas compared to the great tit. Great tits are more active in picking insects from leaves, whilst the flycatchers catch insects in the air (Slagsvold 1975), and may feed frequently on the ground (Sanz 1998), especially in grazed areas (Stowe 1984). The flycatcher may profit from insects in the herbaceous vegetation and among moose dung increasing at the highly fertilized feeding stations, whilst great tits may suffer from reduced leaf and branch density due to browsing in such areas (Persson et al. 2007; Persson et al. 2005). Moose browsing may open up the canopy, increase light availability and increase the abundance of flying insects (Mathisen 2011). The higher occurrence of Lepidoptera in the great tit diet at feeding stations may be caused by a more open and sunlit habitat, and higher flower diversity and abundance at feeding stations (Bergman et al. 2008; Torgersen 2008). A more open habitat and increased abundance of flying insects may be beneficial for flycatchers.

Moose browsing may potentially affect nestling diet quality in addition to quantity of prey, by changing the species composition of different invertebrate prey (den Herder et al. 2009; Suominen et al. 2008). Great tits are known to select for large caterpillar larvae, and the size of larvae has been shown to have a direct positive effect on nestling growth (Naef-Daenzer et al. 2000). Therefore negative effects of high moose browsing on prey size may potentially affect great tit nestling growth. In addition, adult Lepidoptera increased in frequency in the diet at feeding stations. This may indicate a lower quality diet at feeding stations, with a higher ratio of imagoes to larva. These results indicate that moose activity may affect nestling production also through changing diet quality. The other components of the diet showed little difference between nest-box distance classes, but as this was measured at a very coarse taxonomic scale (family level), we cannot rule out differences at lower taxonomic levels.

In this study we have shown that passerine reproduction and habitat selection was affected by the level of moose browsing and nutrient input at supplementary feeding stations. Great tits were negatively affected at high moose activity in accordance with our hypothesis and previous results (Pedersen et al. 2007) whilst contrary to our hypothesis flycatchers were positively affected by high moose activity. This is one of the few studies that have documented effects of large herbivores on passerine reproduction, which may in turn affect population dynamics. The results indicate that high levels of moose browsing pressure may change food availability for small passerines (Pedersen et al. 2007). Although low intensity herbivory may have positive effects on some bird species that prefer open areas (Evans et al. 2006; Loe et al. 2007), high browsing intensity in a low-productive environment most likely has negative effects on bird diversity and reproduction (Fuller 2001), and in some areas this may be a concern for conservation. As there are currently high densities of wild ungulates in many areas (Garrott et al. 1993), indirect effect on other species and trophic levels should be expected. These indirect effects may be hard to predict, as we have seen in this study that two quite similar bird species such as the great tit and the pied flycatcher, react in very different ways to high moose browsing.

Ethical standards
The practices applied in this study comply with the laws of Norway.

Conflict of interest
We have no conflicts of interest.

Supplementary material:

ESM 1 Moose browsing pressure and moose pellet density at the different distances to supplementary feeding stations in the years 2004, 2006 and 2007.

ESM 2 Vegetation and habitat variables at different distance categories to supplementary feeding stations for moose, measured in 2007.

References

Allombert S, Gaston AJ, Martin JL (2005a) A natural experiment on the impact of overabundant deer on songbird populations. Biol Conserv 126 (1):1-13

Allombert S, Stockton S, Martin JL (2005b) A natural experiment on the impact of overabundant deer on forest invertebrates. Conserv Biol 19 (6):1917-1929

Andreassen HP, Gundersen H, Storaas T (2005) The effect of scent-marking, forest clearing, and supplemental feeding on moose-train collisions. J Wildl Manage 69 (3):1125-1132

Bailey JK, Whitham TG (2003) Interactions among elk, aspen, galling sawflies and insectivorous birds. Oikos 101 (1):127-134

Baines D (1996) The implications of grazing and predator management on the habitats and breeding success of black grouse *Tetrao tetrix*. J Appl Ecol 33 (1):54-62

Berger J, Stacey PB, Bellis L, Johnson MP (2001) A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecol Appl 11 (4):947-960

Bergman KO, Ask L, Askling J, Ignell H, Wahlman H, Milberg P (2008) Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. Biodiversity and Conservation 17 (1):139-153. doi:10.1007/s10531-007-9235-x

BoxCar (1997). 3.0 edn. Onset Computer Corporation, Bourne, MA

Brits J, van Rooyen MW, van Rooyen N (2002) Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. African Journal of Ecology 40 (1):53-60

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Cederlund G, Bergström R (1996) Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. In: DeGraaf RM, Miller RI (eds) Conservation of Faunal Diversity in Forested Landscapes. Chapman & Hall, London, pp 265-281

Côté SD, Rooney TP, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Ann Rev Ecol Evol Syst 35:113-147

Cramp S (1977) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Oxford University Press, Oxford

Currie D, Nour N, Adriaensen F (1996) A new technique for filming prey delivered to nestlings, making minmal alterations to the nest box. Bird Study 43:380-382

Danell K, Bergstrom R, Edenius L, Ericsson G (2003) Ungulates as drivers of tree population dynamics at module and genet levels. For Ecol Manage 181 (1-2):67-76

Danell K, Huss-Danell K (1985) Feeding by insects and hares on birches earlier affected by moose browsing. Oikos 44 (1):75-81

Davidson DW (1993) The effects of herbivory and granivory on terrestrial plant succession. Oikos 68 (1):23-35

den Herder M, Bergstrom R, Niemela P, Danell K, Lindgren M (2009) Effects of natural winter browsing and simulated summer browsing by moose on growth and shoot biomass of birch and its associated invertebrate fauna. Ann Zool Fenn 46 (1):63-74

Dhondt AA, Kempenaers B, Adriaensen F (1992) Density-dependent clutch size caused by habitat heterogeneity. J Anim Ecol 61 (3):643-648

Doligez B, Part T, Danchin E (2004) Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Anim Behav 67:457-466. doi:10.1016/j.anbehav.2003.03.010

Evans DM, Redpath SM, Evans SA, Elston DA, Dennis P (2005) Livestock grazing affects the egg size of an insectivorous passerine. Biol Lett 1 (3):322-325. doi:10.1098/rsbl.2005.0335

Evans DM, Redpath SM, Evans SA, Elston DA, Gardner CJ, Dennis P, Pakeman RJ (2006) Low intensity, mixed livestock grazing improves the breeding abundance of a common insectivorous passerine. Biol Lett 2 (4):636-638. doi:10.1098/rsbl.2006.0543

Fuller RJ (2001) Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry 74 (3):289-298

Fuller RJ, Gill RMA (2001) Ecological impacts of increasing numbers of deer in British woodland. Forestry 74 (3):193-199

Garrott RA, White PJ, White CAV (1993) Overabundance - An issue for conservation biologists. Conserv Biol 7 (4):946-949

Gundersen H, Andreassen HP, Storaas T (2004) Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales. Wildlife Biol 10 (3):213-223

Hilden O (1965) Habitat selection in birds. Ann Zool Fenn 2:53-75

Hobbs NT (1996) Modification of ecosystems by ungulates. J Wildl Manage 60 (4):695-713

Holt CA, Fuller RJ, Dolman PM (2010) Experimental evidence that deer browsing reduces habitat suitability for breeding Common Nightingales *Luscinia megarhynchos*. Ibis 152 (2):335-346

Loe LE, Mysterud A, Stien A, Steen H, Evans DM, Austrheim G (2007) Positive short-term effects of sheep grazing on the alpine avifauna. Biol Lett 3 (1):109-111

Luccarini S, Mauri L, Ciuti S, Lamberti P, Apollonio M (2006) Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. Ethol Ecol Evol 18 (2):127-145

Martin JL, Joron M (2003) Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos 102 (3):641-653

Mathisen KM (2011) Indirect effects of moose on the birds and the bees. Sveriges lantbruksuniversitet, Umeå

Mathisen KM, Buhtz F, Danell K, Bergstrom R, Skarpe C, Suominen O, Persson IL (2010) Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. Journal of Vegetation Science 21 (4):705-716. doi:10.1111/j.1654-1103.2010.01180.x

Mathisen KM, Skarpe C (2011) Cascading effects of moose (*Alces alces*) management on birds. Ecological Research 26 (3):563-574. doi:10.1007/s11284-011-0815-6

McShea WJ, Rappole JH (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conserv Biol 14 (4):1161-1170

McShea WJ, Underwood HB, Rappole JH (1997) The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Miller BK, Litvaitis JA (1992) Use of Roadside Salt Licks by Moose, *Alces-Alces*, in Northern New-Hampshire. Canadian Field-Naturalist 106 (1):112-117

Moen A, Lillethun A, Odland A (1999) Vegetation. Norwegian Mapping Authority, Hønefoss

Naef-Daenzer L, Naef-Daenzer B, Nager RG (2000) Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. J Avian Biol 31 (2):206-214

NMI (2008) eKlima. Norwegian Meterological Institute. http://eklima.met.no

Nour N, Currie D, Matthysen E, Van Damme R, Dhondt AA (1998) Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit). Oecologia 114 (4):522-530

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Trends Ecol Evol 13 (7):261-265

Pastor J, Cohen Y (1997) Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. Theoretical Population Biology 51 (3):165-179

Pastor J, Naiman RJ (1992) Selective Foraging and Ecosystem Processes in Boreal Forests. Am Nat 139 (4):690-705

Pedersen S, Nilsen EB, Andreassen HP (2007) Moose winter browsing affects the breeding success of great tits. Ecoscience 14 (4):499-506

Persson I-L (2003) Moose population density and habitat productivity as drivers of ecosystem processes in northern boreal forests. Dr. scient. thesis, Acta Universitatis Agriculturae Suecicae. Silvestria 272 Swedish University of Agricultural Sciences, Umeå

Persson I-L, Bergstrom R, Danell K (2007) Browse biomass production and regrowth capacity after biomass loss in deciduous and coniferous trees: responses to moose browsing along a productivity gradient. Oikos 116 (10):1639-1650

Persson I-L, Danell K, Bergstrom R (2000) Disturbance by large herbivores in boreal forests with special reference to moose. Ann Zool Fenn 37 (4):251-263

Persson I-L, Danell K, Bergstrom R (2005) Different moose densities and accompanied changes in tree morphology and browse production. Ecol Appl 15 (4):1296-1305

Putman RJ, Staines BW (2004) Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. Mammal Rev 34 (4):285-306

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Riipi M, Lempa K, Haukioja E, Ossipov V, Pihlaja K (2005) Effects of simulated winter browsing on mountain birch foliar chemistry and on the performance of insect herbivores. Oikos 111 (2):221-234

Sanz JJ (1998) Effect of habitat and latitude on nestling diet of Pied Flycatchers *Ficedula hypoleuca*. Ardea 86 (1):81-88

Shadish WR, Cook TD, Campbell DT (2002) Experimental and quasi-experimental designs for generalized causal inference. Houghton Mifflin, Boston

Slagsvold T (1975) Competition between the Great tit *Parus major* and the Pied flycatcher *Ficedula hypoleuca* in the breeding season. Ornis Scand 6:179-190

Slagsvold T, Wiebe KL (2007) Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. Anim Behav 73:691-700. doi:10.1016/j.anbehav.2006.05.021

Solbraa K (2002) Veiledning i elgbeitetaksering. Skogbrukets kursinstitutt, Biri

Stewart AJA (2001) The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry 74 (3):259-270

Storaas T, Nicolaysen KB, Gundersen H, Zimmermann B (2005) Prosjekt Elg - trafikk i Stor-Elvdal 2000-2004 hvordan unngå elgpåkjørsler på vei og jernbane. Oppdragsrapport vol 1-2005. Høgskolen i Hedmark

Stowe TJ (1984) Pied Flycatcher and Wood Warbler. Ibis 126 (3):454-454

Suominen O, Danell K (2006) Effects of large herbivores on other fauna. In: Danell K, Bergstrom R, Duncan P, Pastor J (eds) Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, pp 383-407

Suominen O, Persson I-L, Danell K, Bergström R, Pastor J (2008) Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. Ecography 31 (5):636-645

Torgersen S (2008) Effects of moose density and supplementary feeding on field layer vegetation. MSc Thesis, Hedmark University College, Evenstad

van Beest FM, Gundersen H, Mathisen KM, Milner JM, Skarpe C (2010) Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. For Ecol Manage 259:1900-1911

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

Table 1 Estimates from a loglinear mixed model of effects of distance to feeding stations for moose (FS: feeding station, INT: 50-500m from feeding station, FAR: > 500m from feeding station) on number of fledglings produced at weighing for great tits and pied flycatchers. Estimates and standard errors for FS and INT are relative compared to the category FAR.

Species	Distance to FS	Estimate	Std. Error	t value	Pr(>|t|)
Great tit	FAR	2.018	0.0526	38.34	<0.001
	FS	-0.144	0.0846	1.70	0.089
	INT	-0.024	0.0816	0.29	0.769
	Chi square test of distance to feeding station: $\chi^2_{2,73}$=3,12, p = 0,21				
Pied flycatcher	FAR	1.64	0.0819	19.98	<0.001
	FS	0.151	0.102	1.49	0.136
	INT	0.0564	0.107	0.53	0.598
	Chi square test of distance to feeding station: $\chi^2_{2,111}$=2,75, p = 0,253				

Table 2 Linear mixed model of the effects of distance to feeding stations for moose (FS : feeding station, INT : 50-500m from feeding station, FAR : > 500m from feeding station) and year (categorical) on chick weights (g) 2004-2007 for great tits and pied flycatchers, with area/box ID/year as random intercepts. The estimates and standard errors for FS and INT are relative to the category FAR, and the estimates for year are relative to 2004.

Species	Variable	Value	Std. Error	DF	t-value	p-value
Great tit	FAR 2004	15.5	0.654	612	23.62	<.001
	FS	-0.291	0.432	64	0.67	0.504
	INT	-0.200	0.415	64	0.48	0.631
	2005	2.49	0.675	15	3.68	0.002
	2006	2.27	0.702	15	3.23	0.006
	2007	2.38	0.583	15	4.09	0.001
Pied flycatcher	FAR	14.0	0.263	424	53.10	<.001
	FS	0.491	0.266	53	1.85	0.071
	INT	0.692	0.256	53	2.69	0.001

Table 3 Generalized linear mixed model with a quasi-Poisson error correction of daily feeding activity for great tits and pied flycatchers including the effects of distance to feeding station for moose (FS: feeding station, FAR: > 1km from feeding station), day since hatching fitted as a 2-degree polynomial, the interaction day*FS and number of chicks hatched as fixed effects, and box ID as a random effect.

Species	Variable	Value	Std.Error	DF	t-value	p-value
Great tit	FAR	4.88	0.534	218	9.14	<.001
	FS	0.134	0.186	11	0.72	0.485
	Day	0.167	0.0198	218	8.45	<.001
	Day^2	-0.00535	0.000833	218	6.42	<.001
	Hatchlings	0.0677	0.0632	11	1.07	0.307
	FS*day	-0.0198	0.0101	218	1.95	0.052
Pied flycatcher						
	FAR	4.21	0.267	157	15.80	<.001
	FS	-0.139	0.167	8	0.83	0.429
	Day	0.295	0.0260	157	11.35	<.001
	Day^2	-0.0168	0.00143	157	11.71	<.001
	Hatchlings	0.143	0.0408	8	3.51	0.008
	FS*day	0.0270	0.0138	157	1.96	0.051

Table 4 Prey numbers, prey volume and diet composition from filming of nest boxes with great tits to determine nestling diet, at feeding stations (FS) intermediate (INT: 50-500m) and FAR (>500m) from feeding stations for moose. Values given are mean (+/- SE) of number of items delivered to nest boxes during 80 min filming, ratio of arthropod groups in the diet (items per group/total items) and food item volume (see methods for calculation). Difference between FS/INT/FAR was tested with a linear model for volume, and a logistic model for ratios.

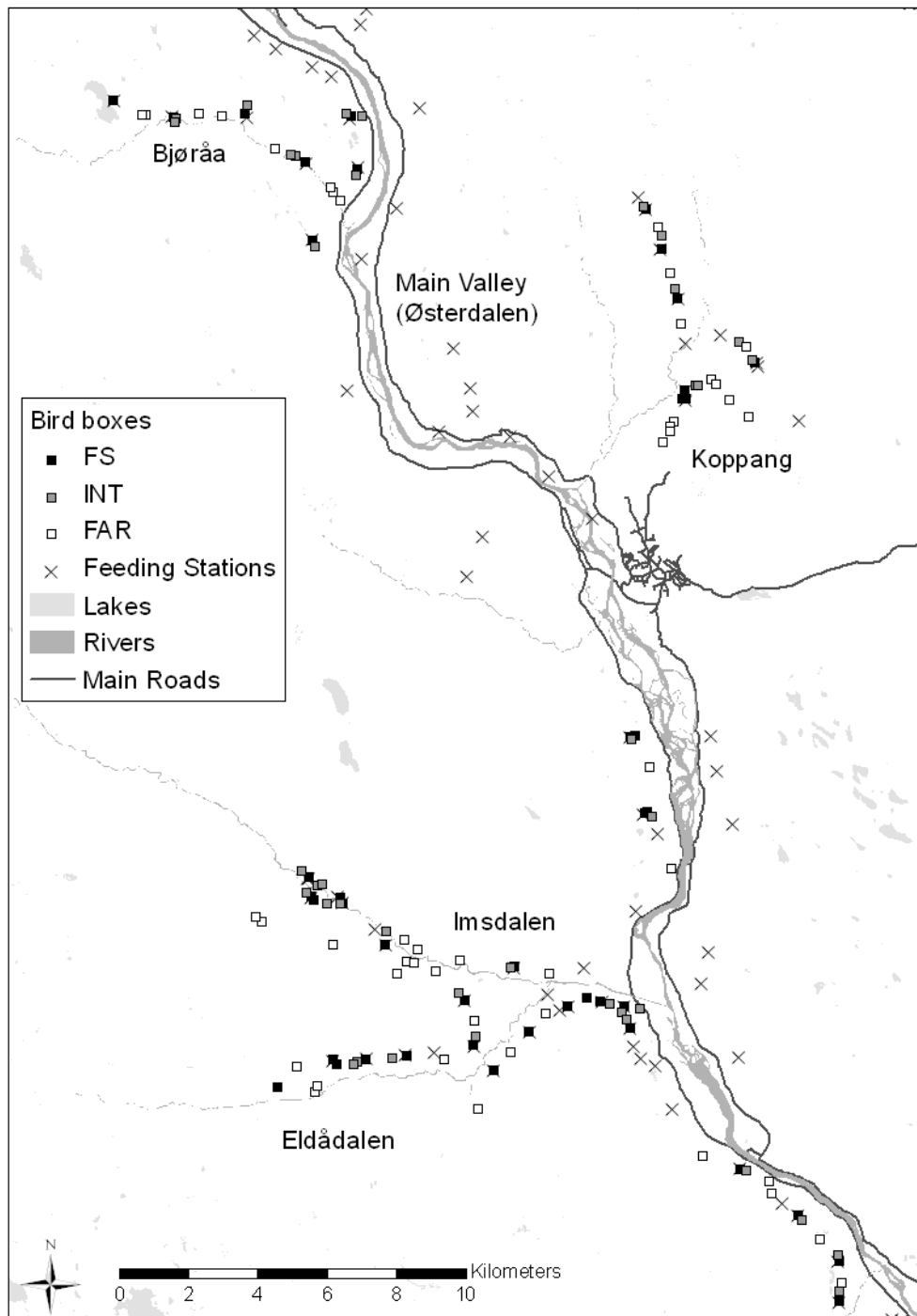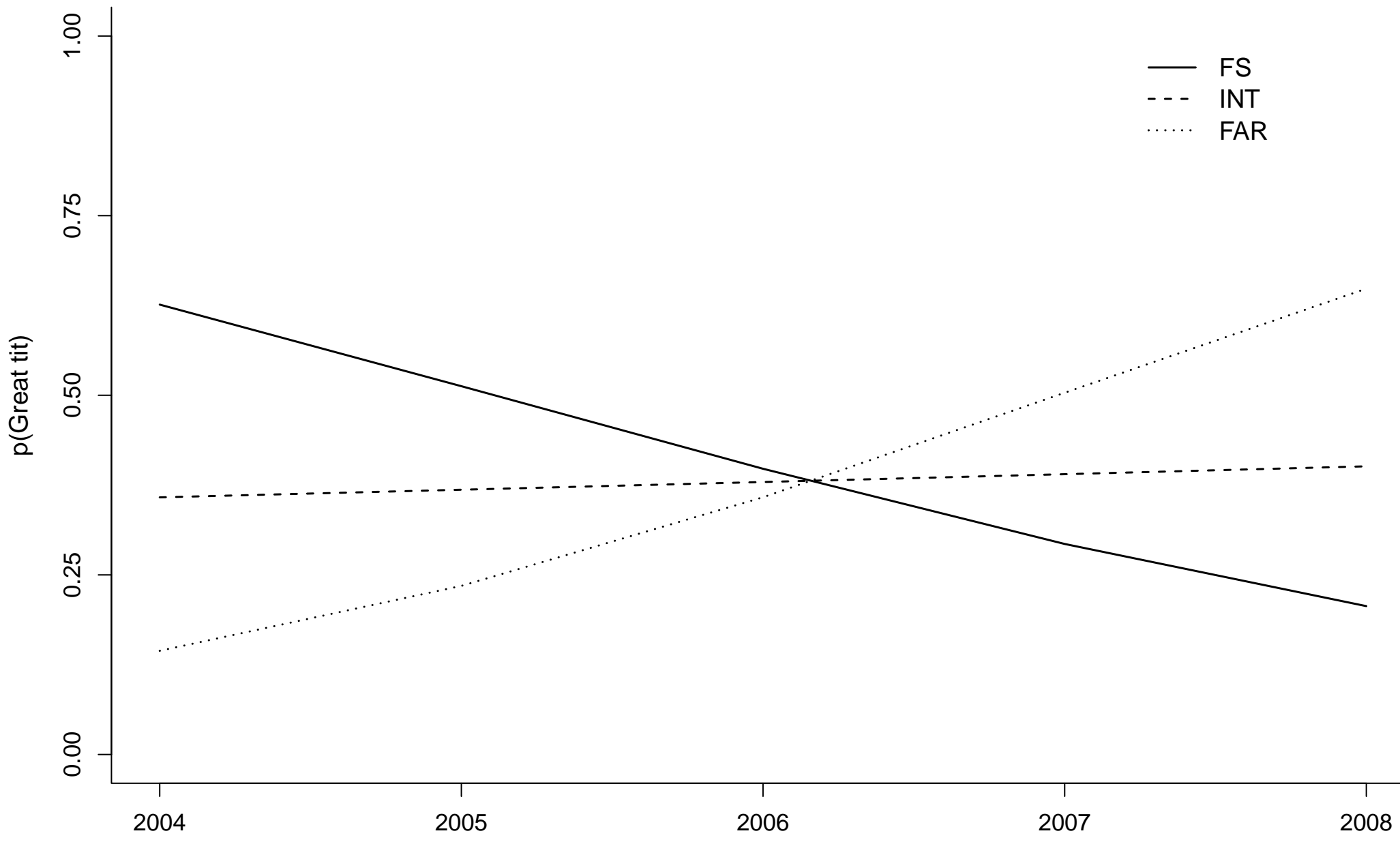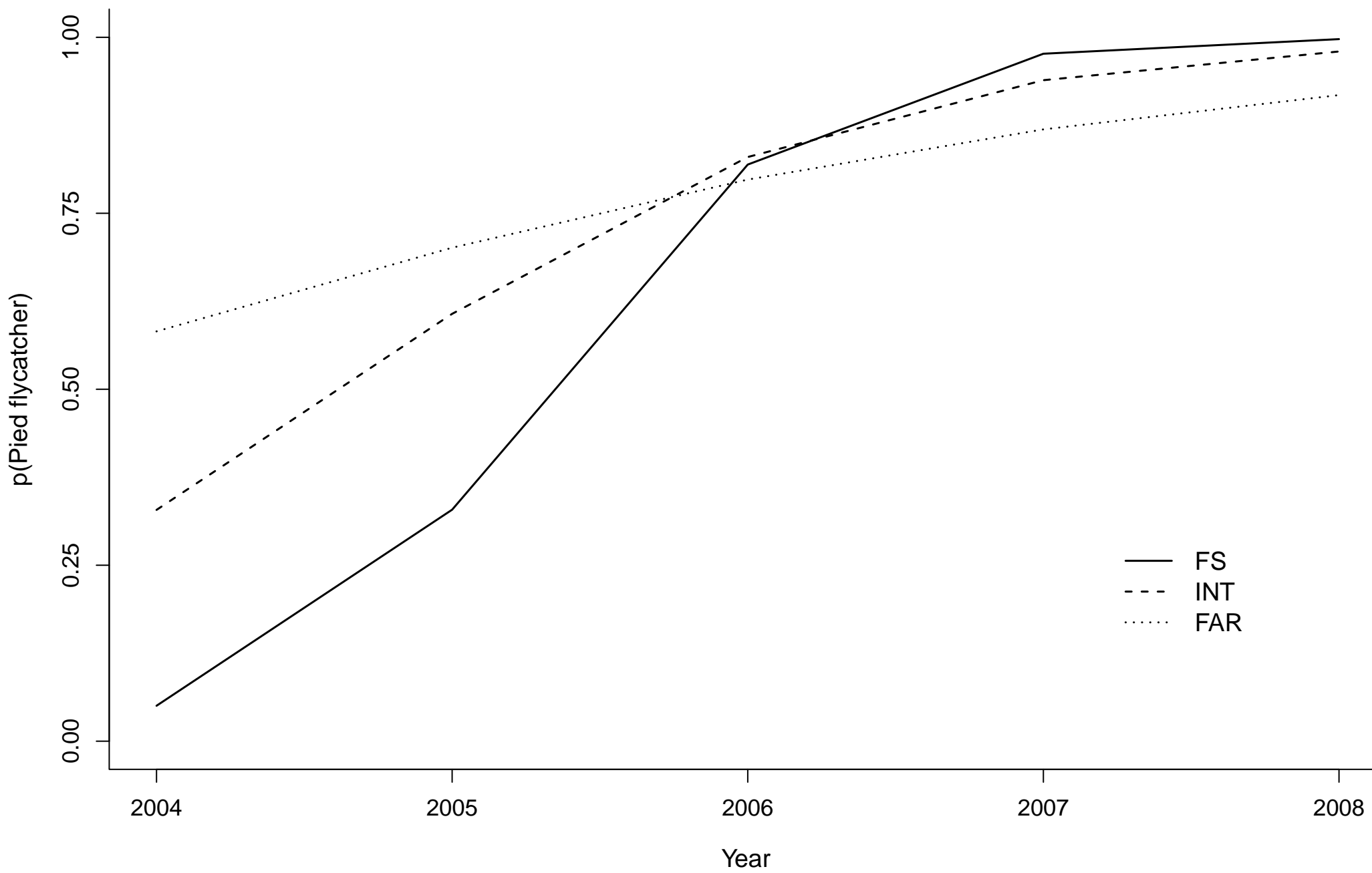| Response variable	FS	INT	FAR	F/Chi^2	p
Total number of prey	30.4 ± 5.68	19.8 ± 6.71	33.4 ± 3.64	$\chi^2_{2,31}=37.55$	0.120
Prey item volume all groups	0.369 ± 0.0760	0.200 ± 0.0597	0.407 ± 0.0831	$F_{2,33} = 0.56$	0.574
Larvae volume Lepidoptera	0.372 ± 0.0978	0.149 ± 0.0266	0.280 ± 0.0333	$F_{2,26} = 1.37$	0.271
Imago Coleoptera	0.150 ± 0.0529	0.165 ± 0.0155	0.145 ± 0.0456	$\chi^2_{2,31} = 1.10$	0.577
Imago Diptera	0.0371 ± 0.0197	0.0176 ± 0.0114	0.0578 ± 0.0393	$\chi^2_{2,31} = 0.55$	0.759
Imago Hymenoptera	0.103 ± 0.0709	0.0563 ± 0.0437	0.0561 ± 0.0233	$\chi^2_{2,31} = 0.39$	0.823
Imago Lepidoptera	0.0840 ± 0.0311	0.0176 ± 0.0114	0.0563 ± 0.0144	$\chi^2_{2,31} = 7.84$	**0.020**
Larvae Coleoptera	0.0364 ± 0.0197	0.0840 ± 0.0296	0.0614 ± 0.0141	$\chi^2_{2,31} = 1.04$	0.595
Larvae Diptera	0.00	0.00	0.0207 ± 0.0196	$\chi^2_{2,31} = 7.82$	**0.020**
Larvae Hymenoptera	0.0786 ± 0.0300	0.190 ± 0.102	0.110 ± 0.0425	$\chi^2_{2,31} = 3.71$	0.157
Larvae Lepidoptera	0.358 ± 0.0931	0.307 ± 0.116	0.375 ± 0.0698	$\chi^2_{2,31} = 1.45$	0.458
Aranea	0.153 ± 0.0551	0.163 ± 0.0701	0.118 ± 0.0174	$\chi^2_{2,31} = 0.86$	0.650
Larvae / Imago ratio all groups	2.17 ± 0.790	2.25 ± 0.446	3.12 ± 0.622	$\chi^2_{2,31} = 2.13$	0.344

Fig. 1 Map over the study area with the distribution of supplementary feeding stations for moose (circles), nest boxes (squares), main valleys, rivers and roads. Nest box distribution is shown for 2007, when the sample size was largest. Boxes were distributed in three distance bands from feeding stations for moose: at feeding stations (FS), intermediate distance (INT: 50-500m) and FAR from feeding stations (> 500 m).
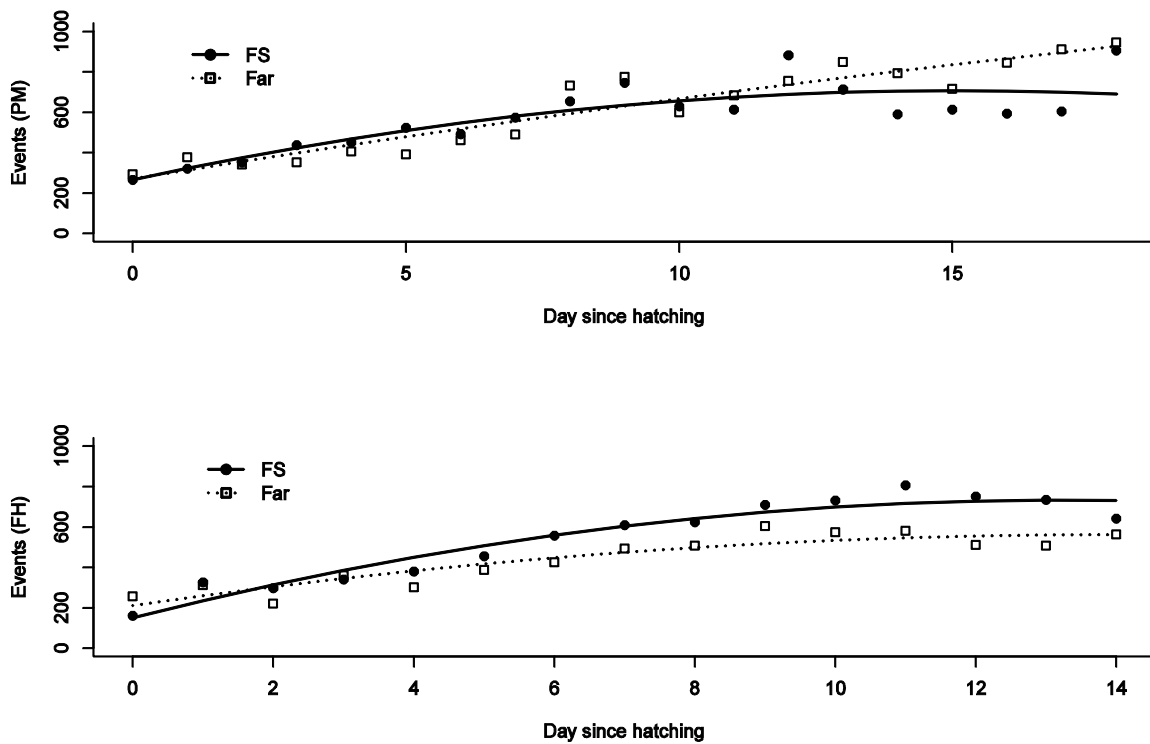
Nest box occupation

Fig. 3 Number of feeding trips per day estimated from activity loggers (in 2007) as a function of day since hatching for nest boxes with chicks of great tits (above) and pied flycatchers (below) at feeding stations (FS) for moose and > 1km from feeding station for moose (FAR).

Supplementary material :

ESM 1 Moose dung and browsing (mean % browsed shoots/available shoots ± SE) around bird-boxes at feeding stations for moose (FS), intermediate distance (INT: 50-499 m from feeding stations) and FAR distance (> 500 m from feeding stations). The effect of distance to feeding station, year (factor) and the interaction between them on moose browsing of the 3 dominating tree species was analyzed using a GLMM with binomial errors and Box ID nested within area as random effects. Moose pellet groups was analyzed using a GLMM with a quasipoisson error correction and the same random structure.

Mean values and SE				Analysis	
Year	FS	INT	FAR	x-Variable	Test statistics
Pellet groups per m^2					
2004	0.357 ± 0.0854	0.0145 ± 0.00330	0.00800 ± 0.00240	FS/Int/Far	$X^2_2 = 129.95$, p <.001
2006	0.728 ± 0.0941	0.0539 ± 0.0127	0.0210 ± 0.00446	Year	$X^2_2 = 1589$, p <.001
2007	0.321 ± 0.0486	0.0229 ± 0.00320	0.0107 ± 0.00156	FSIntFar*year	$X^2_4 = 7.53$, p = 0.110
Birch browsing (%)					
2004	78.2 ± 2.16	37.8 ± 5.58	13.3 ± 4.84	FS/Int/Far	$X^2_2 = 62.08$, p <.001
2006	80.7 ± 3.89	61.3 ± 4.76	47.5 ± 8.79	Year	$X^2_2 = 2725$, p <.001
2007	97.0 ± 0.92	81.0 ± 3.64	77.1 ± 3.41	FSIntFar*year	$X^2_4 = 125.7$, p <.001
Pine browsing (%)					
2004	83.3 ± 0.00	58.7 ± 7.53	61.1 ± 13.6	FS/Int/Far	$X^2_2 = 4.78$, p = 0.092
2006	69.2 ± 3.91	59.8 ± 4.58	42.8 ± 17.6	Year	$X^2_2 = 1570$, p <.001
2007	96.1 ± 2.02	91.3 ± 2.55	90.3 ± 2.81	FSIntFar*year	$X^2_4 = 71.20$, p <.001
Spruce browsing (%)					
2004	23.1 ± 7.62	1.92 ± 1.29	0.00 ± 0.00	FS/Int/Far	$X^2_2 = 5487$, p <.001
2006	53.4 ± 4.81	17.4 ± 3.32	4.50 ± 2.06	Year	$X^2_2 = 1483$, p <.001
2007	68.0 ± 5.40	29.1 ± 4.92	8.10 ± 1.53	FSIntFar*year	$X^2_4 = 46.85$, p <.001

ESM 2 Distribution of nest-boxes in the different forest age classes and vegetation types and mean (+/- SE) of vegetation variables measured in 2007 around nest boxes at FS (feeding station for moose), INT (50-500m from FS) and FAR (> 500m from FS). Differences among categories were tested with a one-way ANOVA for vegetation variables, and a chi-square test for forest age class and vegetation type. RSA: Rowan, *Salix* spp. and Aspen (grouped).

Variable	FS	INT	FAR	Test statistic	p
Forest age classes (number of boxes)					
Clear-cut	3	0	1	$\chi^2 = 3.95$	0.684
≤ 8m height	21	20	24		
> 8m height	15	15	18		
Mature forest	4	4	3		
Vegetation types (number of boxes)					
Lichen	1	3	5	$\chi^2 = 5.02$	0.755
Cowberry & bilberry	18	19	21		
Heather & bog-bilberry	7	5	8		
Bilberry	10	7	9		
Small-fern	7	5	3		
Tree canopy cover (%)					
Pine > 3m height	8.16 ± 1.67	10.1 ± 1.82	12.7 ± 2.22	$F_{2,125} = 1.09$	0.341
Pine < 3m height	0.628 ± 0.136	0.872 ± 0.131	1.08 ± 0.151	$F_{2,125} = 3.86$	0.024
Spruce > 3m height	10.6 ± 2.45	8.68 ± 1.62	8.67 ± 1.37	$F_{2,125} = 0.04$	0.960
Spruce < 3m height	4.38 ± 0.653	3.14 ± 0.420	3.59 ± 0.583	$F_{2,125} = 0.56$	0.574
Birch > 3m height	9.72 ± 1.54	21.6 ± 3.45	9.13 ± 1.09	$F_{2,125} = 8.15$	<.001
Birch < 3m height	10.1 ± 1.72	6.87 ± 1.02	9.48 ± 1.45	$F_{2,125} = 1.60$	0.206
RSA > 3m height	2.47 ± 1.87	0.410 ± 0.220	0.500 ± 0.366	$F_{2,125} = 1.20$	0.306
RSA < 3m height	3.02 ± 0.641	2.53 ± 0.811	1.79 ± 0.415	$F_{2,125} = 1.19$	0.308
Field layer vegetation cover(%)					
Lichens	16.9 ± 2.42	23.5 ± 3.14	22.8 ± 2.49	$F_{2,125} = 2.52$	0.085
Herbs and grasses	34.8 ± 4.62	14.1 ± 3.05	13.4 ± 3.32	$F_{2,125} = 10.55$	<.001
Dwarfshrubs	37.6 ± 3.60	52.9 ± 3.62	53.0 ± 3.88	$F_{2,125} = 5.36$	0.006
Elevation	482 ± 20.5	454 ± 17.3	486 ± 19.9	$F_{2,125} = 0.17$	0.843