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Effects of native and introduced cervids on small mammals and birds

Thesis for the degree of Philosophiae Doctor

Trondheim, November 2011

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ISBN ISBN 978-82-471-3240-1 (printed ver.)
ISBN ISBN 978-82-471-3241-8 (electronic ver.)
ISSN 1503-8181

Doctoral theses at NTNU, 2011:328

Printed by NTNU-trykk

Dedicated to the memory of my grandmother Ruth Pedersen

Preface

This thesis is no one man's work, there is a long list of people that have contributed. The most important are my three supervisors Christina Skarpe, Harry Andreassen and Eivin Røskaft that have been great discussion partners, and provided advice. Christina I appreciate your quick and thorough response to manuscript drafts, often within the next day! I'd especially like to thank you Harry for helping me whenever I got stuck in data analysis, and for your clear thinking. Eivin, you have an amazing way of telling me I need to speed up while focusing on the positive, no matter how dark my mind was when entering your office, I felt like superman when leaving.

Thanks also to my fellow PhD students / post docs. at Evenstad (Karen Marie Mathisen, Lucrezia Gorini, Alice Remy, Lasse Asmyhr, Petter Glorvigen, Kim Magnus Bærum, Clara Valente and Mikkel Kvasnes), in Trondheim (Iddi Mfunda, Dennis Ikanda and Tomasz Ciesielski), and Tino Schott in Tromsø for discussions in and outside the office. The weeks of working alongside you Alice this summer in our common race for the deadline was inspiring. I'd also like to thank my other colleagues at Evenstad for discussions and a good working environment, and especially Torstein Storaas for involving me in other interesting projects. Karen Marie and Lucrezia thanks for our collaboration on the paper(s), I hope there are more to come.

Getting an invitation to go to Australia to do a research project with you Clare McArthur was something I truly loved, thank you for your hospitality. I'm also grateful to the others involved in the Australian project for good collaboration; Iain Gordon, David Keith, Matthew Crowther, Glenda Wardle and Chris Dickman. Being able to work in the exclosures and with the people in Umeå was a great opportunity. Thank you Inga-Lill Persson, I hope our further collaboration will be fruitful. I'd also like to thank Riitta Julkunen-Tiitto and Kjell Danell for our collaboration on the café paper. Erlend Nilsen thank you for a great collaboration on the moose-bird papers and for involving me in other fun projects. Having field assistants is a luxury, thank you all for the endless hours of work you've put down on these various projects.

I'm indebted to Hedmark University College for funding my PhD and the Norwegian Research Council, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), the Swedish Environmental Protection Agency and University of Sydney for co-funding parts of the various projects. I'm also grateful to the landowners and landowner associations for providing various information and allowing me to work on their properties.

Thanks also to my hunting buddies Eirik Seim, Geir Nordgaard, Svein Gjennestad, Bjørn Sverre Ekran, Ulf Sørumgård, Jon Erling Brænd, Tomasz, Hans Chr Pedersen, and Klinge for dragging me out of the office, detaching my mind from browsing and statistics.

Getting interested in ecology and research in the first place is all due to my father, Hans Christian, I admire you. Thank you for showing me the ways of the ptarmigan in Gåvålia and spark my curiosity for ecology. I also thank my mother Kari and sister Guro for being supportive and encouraging throughout. I would also like to thank my parents for looking after my daughters during the last couple of weeks of writing, it helped a lot.

Finally, I thank my wife Lisbeth for being loving, supportive and understanding, especially during the last intensive period of writing. Our two daughters Oda and Vårin have taught me so much about life and helped me put things into perspective. I hope I can teach you Oda and Vårin the love of nature and curiosity that my parents taught me. I ask for forgiveness to my whole family for being physically and mentally absent for the past months, I love you all.

Klinge, get ready…

Koppang / Trondheim, October 2011 Simen Pedersen

Contents

List of individual papers

This thesis is based on the following papers, hereafter referred to by their roman numerals:

I S Pedersen, HP Andreassen, I-L Persson, R Julkunen-Tiitto, K Danell and C Skarpe. (2011). Vole preference of bilberry along gradients of simulated moose density and site productivity. Integrative Zoology 6: 342-352. DOI: 10.1111/j.1749-4877.2011.00260.x

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

III KM Mathisen, S Pedersen, EB Nilsen and C Skarpe (manuscript). Contrasting responses of two passerine bird species to moose browsing. (submitted to European Journal of Wildlife Research).

IV S Pedersen, KM Mathisen, L Gorini, HP Andreassen, E Røskaft and C Skarpe (manuscript). Small mammal responses to moose supplemental winter feeding.

V S Pedersen, HP Andreassen, DA Keith, C Skarpe, CR Dickman, IJ Gordon, MS Crowther and C McArthur (manuscript). The relationship between small mammals and native and introduced large herbivores in coastal heathland.

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Declaration of contribution

All authors commented on the manuscript drafts.

Paper I, I collected and analyzed the data and wrote the manuscript, CS and I-LP had the idea, RJ-T ran the chemical analysis, while KD initiated the exclosure study. I-LP, RJ-T and KD provided data on bilberry chemical composition.

Paper II, I collected and analyzed the data and wrote the manuscript, EBN and HPA had the idea and assisted in data analysis, while EBN contributed in the field.

Paper III, KMM collected and analyzed the data and wrote the manuscript, while I and EBN contributed with data and ideas, CS commented on the manuscript.

Paper IV, I had the idea, collected and analyzed data and wrote the manuscript, KMM and LG contributed to the planning and field work, CS, HPA and ER commented on the manuscript.

Paper V, I collected and analyzed the data and wrote the manuscript, I and CMA had the idea and planned the study together with CRD, MSC, DAK, IJG and HPA, HPA also provided statistical advice, while CS commented on the manuscript.

Summary

Cervids are a widespread family of ungulates, native to the Americas, Europe and Asia and introduced to Australia. Densities of cervids have increased in North America, Europe and Japan during the last couple of decades, due to changes in land use, reduced hunting, lack of large carnivores and changes in management practices. Where they occur at high densities, native and introduced cervids may have profound effects on vegetation, causing knock-on effects on other taxa. Cervids are in some instances managed towards changing the local distribution through supplemental feeding. These supplemental feeding stations are causing localized areas of high cervid abundance in the landscape, and may have effects on plants and animal species.

In this thesis I investigate how high cervid densities and the practice of supplemental feeding impact birds and small mammals through effects on; 1) food resources, and 2) habitat structure.

Utilizing a simulated moose (*Alces alces*) browsing experiment, I tested how varying moose densities and varying site productivity affects vole preference for bilberry. I found that voles preferred unbrowsed bilberry at low productivity sites, while they preferred lightly browsed bilberry at high productivity sites, I was however unable to explain the preference pattern with the chemical composition of the bilberry. However, moose do impact vole food preferences and this could, depending on the productivity of the site, potentially affect food selection and population dynamics over large geographical areas.

Moose browsing pressure and nutrient input gradually decline with distance from supplemental winter feeding stations. I utilized this gradient to test how moose activity affects reproduction in pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*). The two species showed contrasting responses to moose feeding stations, great tits preferred to nest away from feeding stations where they showed higher feeding frequency and also produced more fledglings compared to close to feeding stations. Pied flycatchers on the other hand preferred to nest close to feeding stations where they had higher feeding frequency and fledgling mass was higher compared to further away. Hence, for both

species moose browsing is affecting food availability that subsequently affects reproductive performance.

Moose supplemental feeding stations also changed the habitat for small mammals from dwarf shrub dominated to grass and forb dominated. This did not have any effect on reproductive performance of the small mammals, but it did affect species composition along a gradient from the feeding stations. There was higher abundance of *Microtus* spp. and common shrews (*Sorex araneus*) close to feeding stations, while bank voles (*Myodes glareoleus*) had higher abundance away from feeding stations, the latter however was not statistically significant.

Small mammals in Australian coastal heath were generally negatively associated with introduced rusa deer (*Cervus timorensis*), however one species responded positively to historical densities of rusa deer. It was however not possible to confirm these effects as being due to changes in habitat structure for the small mammals. However they may be explained by qualitative changes in the vegetation or alternatively by direct effects of deer through trampling or predation.

Cervids and their management have an impact on other fauna, however the effects vary depending on small mammal and bird species. The effects of cervids also depend on the habitat requirements and foraging preferences of the small mammals and birds. Effects may be mediated through both food resources and habitat structure and are dependent on site productivity and cervid density.

Introduction

Cervids are a widespread family of ungulates, native to the Americas, Europe and Asia. They have been introduced to Australia over the past two centuries, and are represented by only one native species in the bovid-dominated continent of Africa. Densities of native cervids have increased in North America, Europe and Japan during the last couple of decades (McShea et al. 1997; Côté et al. 2004; Takatsuki 2009). The reasons for these population increases are complex including changes in land use (Edenius et al. 2002; Takatsuki 2009), reduced hunting effort (Côté et al. 2004; Takatsuki 2009), lack of large carnivores (Wabakken et al. 2001; Takatsuki 2009), and changes in management practices (Solberg et al. 1999). Cervids are the most commonly introduced family of ungulates (Spear & Chown 2009) and have historically been introduced and continue to be introduced to new locations outside their native range for reasons such as sport hunting, deer farming or to "enhance the aesthetics of the local environment" (Moriarty 2004a; Dolman & Waber 2008). Where they occur at high densities, native and introduced cervids may have profound impacts on the vegetation which in turn may cause knock-on effects on other taxa (McShea & Rappole 1997; Suominen & Danell 2006; Dolman & Waber 2008; Spear & Chown 2009). Cervids are in some instances managed towards changing local distribution through supplemental feeding, in order to e.g. reduce negative impacts on economically important plant species or reduce cervid-vehicle collisions (Gundersen et al. 2004; Putman & Staines 2004; van Beest et al. 2010). The supplemental feeding stations are causing localized areas of high cervid densities in the landscape. These high densities and the added plant biomass in the system, may have effects on plants and other animal species (e.g. Mathisen & Skarpe 2011).

Large herbivores cause direct effects on the vegetation though browsing or grazing, trampling, urination and defecation (Hobbs 1996). Numerous studies have focused on the effects of herbivory on plant species composition and on structural and chemical changes in the plants (Herms & Mattson 1992; Hester et al. 2006; Skarpe & Hester 2008, and references therein). Recently however, there has been an increased focus on the indirect effects that large herbivores may have on invertebrates (Suominen et al. 1999; den Herder et al. 2004; Allombert et al. 2005a; Melis et al. 2006a; Melis et al. 2006b; Suominen et al. 2008; den Herder et al. 2009), birds (Evans et al. 2006; Holt et al.

2011; Mathisen & Skarpe 2011) and small mammals (Keesing 1998; Saetnan & Skarpe 2006; Johnston & Anthony 2008; Pringle et al. 2010; Buesching et al. 2011). For invertebrates and birds the effects vary depending on the functional group as well as the species of large herbivore, its density and feeding type (i.e. browser or grazer) (Evans et al. 2006; Melis et al. 2006b; Suominen et al. 2008; Mathisen & Skarpe 2011). The responses of small mammals however are surprisingly consistent despite variation in small mammal species and in the species and densities of large herbivores. The overall pattern is a negative effect of large herbivores on small mammals (Keesing 1998; Saetnan & Skarpe 2006; Johnston & Anthony 2008; Buesching et al. 2011).

To focus this synthesis, and to foreshadow the research that has been carried out in this thesis, I next consider cervid impacts on small homeoterms. There are several non-mutually exclusive ways that cervids may influence birds and small mammals indirectly or directly. Indirect effects are caused by interwoven changes in; i) food resources, and ii) habitat structure affecting small mammals and birds, or their invertebrate prey. Direct effects include trampling of nests or animals and predation. In this thesis I will focus on the indirect effects of high cervid densities on; i) food resources, and ii) habitat structure.

Effects of cervids on food resources

One way high cervid densities might influence small herbivores in the community is by changing the palatability and nutritional quality of food plants caused by herbivory at the individual plant or feeding site scale (*sensu* Johnson 1980). Previous herbivory may either increase (Danell & Huss-Danell 1985; Danell et al. 1985; Skarpe et al. 2000; Makhabu et al. 2006) or decrease (Bryant et al. 1994; Duncan et al. 1998) herbivore preference for a plant. According to the *grazing facilitation hypothesis* large species improve the foraging opportunities for smaller species by modifying plant biomass and structure (Bell 1971). The *grazing facilitation hypothesis* has also been suggested to apply to browsing systems, where smaller browsers may benefit from regrowth that has been stimulated by earlier browsing from large herbivores (Makhabu et al. 2006; Valeix et al. 2011). Facilitation by large herbivores may lead to increased preference by small herbivores for compensatory regrowth. This could arise as a result of browsing removing many meristems[1] leading to reduced number of shoots the following growing season. Hence, more nutrients are available to each shoot, which then grow rapidly and contain less structural tissue (i.e. cellulose or lignin) and also less chemical defense[2] (Skarpe & Hester 2008). Decreased preference might be caused by plants producing secondary metabolites that are; 1) unpleasant tasting to the herbivore, 2) digestive inhibitors, or 3) toxic (Bryant et al. 1992). Thus there will be high selection pressure against feeding on heavily defended plants. The plant response can also depend on an interaction between the productivity of the site and browsing (Strengbom et al. 2003). The *growth differentiation balance hypothesis* has been interpreted as plants at; 1) low productivity sites have limited resources to put into both defense and growth, 2) sites of intermediate productivity allocate more resources to defense while growth is moderate, and 3) high productivity sites put more resources into growth and less so into defense (Herms & Mattson 1992; Stamp 2003). Facilitation would thus be expected primarily at high-productivity sites. Reindeer (*Rangifer tarandus*) have been shown to be associated with high densities of small mammals, thus suggesting a facilitating effect (Ims et al. 2007). Sheep (*Ovis aries*) grazing has also been shown to facilitate grazing for rodents (Austrheim et al. 2007). Steen et al. (2005) found that whereas high densities of sheep were negative to population growth rate of field voles (*Microtus agrestis*), intermediate densities had a facilitating effect on population growth rate. On the other hand bank voles (*Myodes glareolus*) were not affected by sheep densities (Steen et al. 2005).

Cervids may affect food plants that are available to invertebrates, either quantitatively or qualitatively, and invertebrate populations may then respond to these changes either positively (Danell & Huss-Danell 1985; Roininen et al. 1997) or negatively (Bailey & Whitham 2003; den Herder et al. 2004; den Herder et al. 2009). Subsequently, insectivorous small mammals and birds may respond to changes in invertebrate abundance and assemble composition that indirectly is caused by cervid herbivory.

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[1] Meristems are points of new growth in plants, from which shoots may grow.

[2] Plant defense is either constitutive or induced, constitutive defense is static and not influenced by herbivory, while induced defense is triggered by herbivory or other damage.

Effects of cervids on habitat structure

On the home range scale (*sensu* Johnson 1980), cervids may alter the structural complexity of habitat housing birds and small mammals. Cervid-induced reductions in vertical and horizontal habitat complexity are known to have negative impacts on bird diversity and density by reducing cover from predators and foraging substrate (McShea & Rappole 1997). deCalesta (1994) found that bird species nesting at intermediate heights (< 7.5 m) were affected negatively by high densities of white-tailed deer (*Odocoileus virginianus*) whereas species nesting on the ground or in the upper canopy were not affected, this was presumably because the percent ground cover and upper canopy were unaffected by deer. Deer-induced habitat changes also have an effect on small mammal densities by reducing the amount of cover from predators (Flowerdew & Ellwood 2001). For example tawny owls (*Strix aluco*) have higher predation success on wood mice (*Apodemus sylvaticus*) in parts of their territories where ground cover is low compared to where it is dense (Southern & Lowe 1968).

Large herbivores may have substantial effects on invertebrates through changes in habitat structure (Suominen et al. 1999; Allombert et al. 2005a; Melis et al. 2006a; Melis et al. 2006b; Suominen et al. 2008). The direction and strength of the effects vary depending on the habitat requirements of invertebrates and the severity of impact by the large herbivore. By changing habitat structure large herbivores may therefore also indirectly affect insectivorous small mammals and birds. Putman et al. (1989) found that the abundance of insectivorous shrews were affected negatively by grazing, possibly as a consequence of reduced habitat complexity resulting in decreased invertebrate abundance. Several studies have also suggested that reduced arthropod abundance mediated though habitat changes by cervids can cause reduced bird species diversity (Fuller 2001; Allombert et al. 2005b; Holt et al. 2011).

Aim of thesis

Densities of large herbivores are high in many parts of the world, and have the potential to profoundly affect vegetation and concurrently many other taxa. In this thesis I investigate the impacts of high densities of native and introduced large herbivores and the management thereof on birds and small mammals. This topic has received increasing focus in the past decade, but knowledge is still incomplete with much research to be done.

My general aim was addressed by focusing on the following research questions:

- How do cervid densities affect food quality available to small mammals? (Paper I)
- How do cervid densities and management actions affect habitat structure available to birds? (Papers II and III)
- How do cervid densities and management actions affect habitat structure available to small mammals? (Papers IV and V)

Methods

Study areas

The collection of field data was done in three separate study areas, two in Scandinavia; Umeå, Västerbotten, northern Sweden (63° N, 20° E) (Paper I) (Figure 1) and Stor-Elvdal, Hedmark, southeastern Norway (61°N, 11°E) (Papers II, III and IV) (Figures 1; 2) and one in Royal National Park, New South Wales, southeastern Australia (34°S, 151° E), (Paper V; Figure 3). The two sites in Scandinavia are located in the boreal forest, while the study area in Australia is located in coastal heath. Scandinavia and Australia differ in how they are influenced by important abiotic factors. While the boreal forest in Scandinavia is affected by logging, Australian coastal heath is burned periodically by wildfires or prescribed burns. Both these factors operate over extensive areas and can have large impacts on the respective ecosystems.

Figure 1. The two study systems in Scandinavia; Stor-Elvdal municipality, Hedmark County, SE Norway and Umeå, Västerbotten County, NE Sweden.

Umeå study system (Paper I)

To determine how moose (*Alces alces*) densities affect food quality to voles, I made use of a simulated moose density experiment established in 1999. The system consists of eight fenced exclosures along a productivity gradient. Each exclosure consists of four treatment plots of 25 m by 25 m where simulated browsing, defecation and urination have been carried out according to four different moose population densities (0, 1, 3 and 5 moose per km^2) corresponding to the range of known moose densities in Fennoscandia. Simulated moose densities were allocated randomly to the treatment plots. The removal of plant biomass from the plots was calculated based on known daily consumption in winter and summer (Persson et al. 2000), and on known diet composition throughout the year (Cederlund et al. 1980). Moose dung and artificial urine was added according to the simulated density in the respective plot, based on known urination and defecation rates (Persson et al. 2000). For each exclosure a site productivity index was calculated (Persson et al. 2007; Suominen et al. 2008; Persson et al. 2009). See Paper I for more details on the study system.

Stor-Elvdal study system (Papers II, III and IV)

Here I investigated the effects of high moose densities and supplementary winter feeding of moose on habitat structure available to passerine birds (papers II and III), and small mammals (Paper IV). Moose densities in Stor-Elvdal municipality range from 1.1 to 3.4 moose per km^2 (Gundersen et al. 2004; Storaas et al. 2005). In order to prevent forest damage and vehicle collisions moose have since 1990 been fed ensilaged grasses and roughage at supplementary feeding stations during winter (Gundersen et al. 2004; Figure 2). Moose aggregate around these feeding stations giving rise to areas in the landscape with high browsing intensity and nutrient input. Browsing and nutrient input through dung, urine and silage remains is high at feeding stations and declines with distance, but not at the same scale. While browsing pressure remains fairly high up to approximately 200 m from feeding stations (van Beest et al. 2010), the amount of feces and presumably nutrient input drops rather abruptly after approximately 50 m from the feeding stations. In Papers II and III I utilized the distance to feeding stations as a proxy for varying moose densities, while in Paper IV I investigated the effects of the management practice of supplementary winter feeding of moose. This type of study system is not strictly experimental, as treatments are not allocated randomly, but rather belongs to a group of studies termed quasi-experimental which are highly structured observational studies (Shadish et al. 2002). I divided the distance from feeding stations into different distance categories depending on the study (Figure 2); see Papers II, III and IV for details.

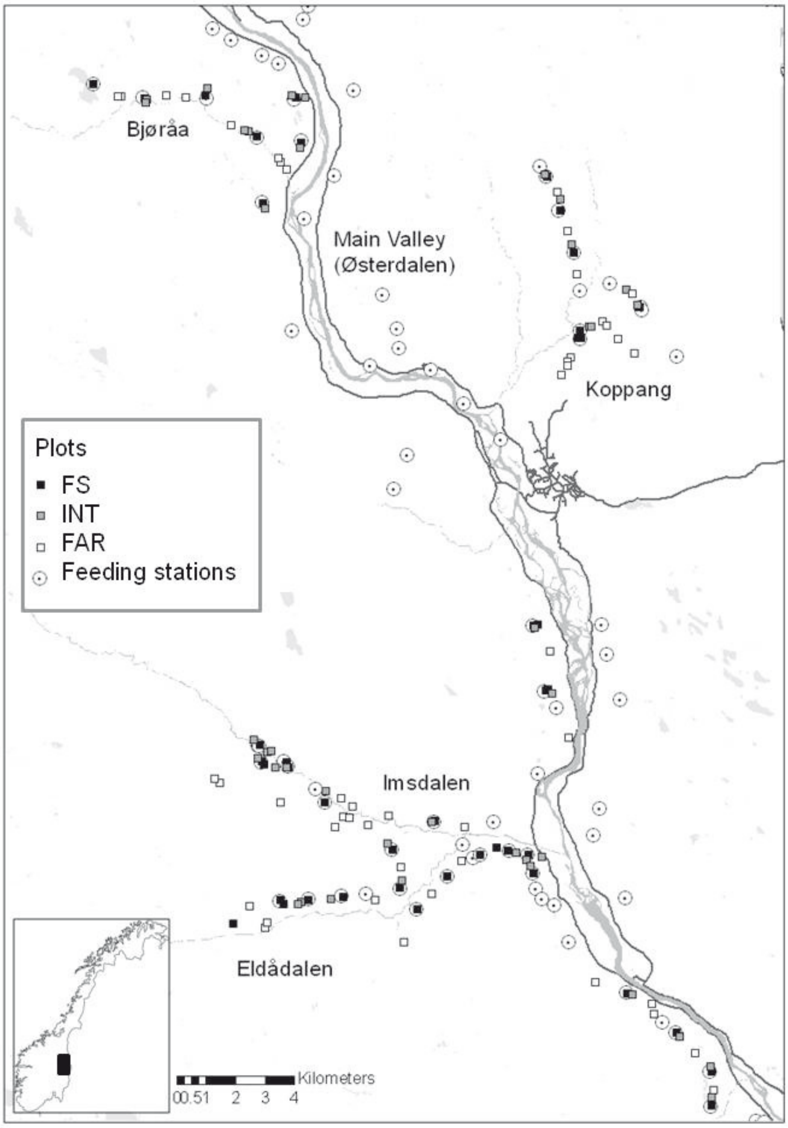

Figure 2. Map of the Stor-Elvdal study area (Papers II, III and IV) with the distribution of supplementary winter feeding stations for moose (circles), study plots (squares), main rivers and roads. Plot distribution is from Paper III in 2007 when the number of study plots was highest, studies reported in Papers II and IV were conducted at a subset of the plots shown in this map. Plots are distributed in three distance bands from the feeding stations; at feeding stations (FS), intermediate distance (INT; 50 - 500 m), and far from feeding stations (FAR > 500 m).

Royal National Park study system (Paper V)

Here I investigated the relationship between small mammals and changes in habitat structure induced by large herbivores. Rusa deer (*Cervus timorensis*), native to parts of Indonesia was introduced by acclimatization societies[3] to Australia at the beginning of the 20th century. The deer spread and has established within the Royal National Park, and surrounding areas (Keith & Pellow 2005). Herbivory and environmental degradation caused by feral deer is listed as a Key Threatening Process under the New South Wales government *Threatened Species Conservation Act 1995*. (www.environment.nsw.gov.au, accessed June 14th 2011). Swamp wallabies (*Wallabia bicolor*) are the only native large herbivore present in the park. By conducting pellet counts and using old records of deer and wallaby density, I was able to classify 33 sites within the park according to past and present large herbivore use, and correlated this with small mammal captures (Figure 3).

Study species

In Papers I and IV, I studied the impacts of moose browsing and moose feeding stations on small mammals, specifically common shrew (*Sorex araneus*), *Microtus* species and bank voles. These species differ in their habitat preferences. Bank voles inhabit dwarf shrubs generally, and bilberry especially in Scandinavia (Selås 2006). *Microtus* spp. and common shrews on the other hand are associated with productive grass-dominated vegetation in the field layer (Hanski & Kaikusalo 1989; Panzacchi et al. 2010).

In Papers II and III, I studied great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). These are cavity nesting insectivorous passerine bird species that are common throughout the boreal forest and are willing to use artificial nestboxes. They differ somewhat in their feeding preferences, great tits are arboreal feeders, whereas flycatchers forage more on the ground or in the air (Slagsvold 1975; Sanz 1998).

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[3] Acclimatization societies were created by European colonists to enrich the local fauna with new species, particularly species that were familiar from Europe and pleasing to the eye.

In Paper V, I studied a suite of small mammal species in Australian coastal heath; the omnivorous New Holland mouse (*Pseudomys novaehollandiae*), insectivorous brown antechinus (*Antechinus stuartii*), omnivorous bush rat (*Rattus fuscipes*) and herbivorous swamp rat (*R. lutreolus*). These species have different habitat preferences and thus I expected them to show a range of different species-specific responses to large herbivores.

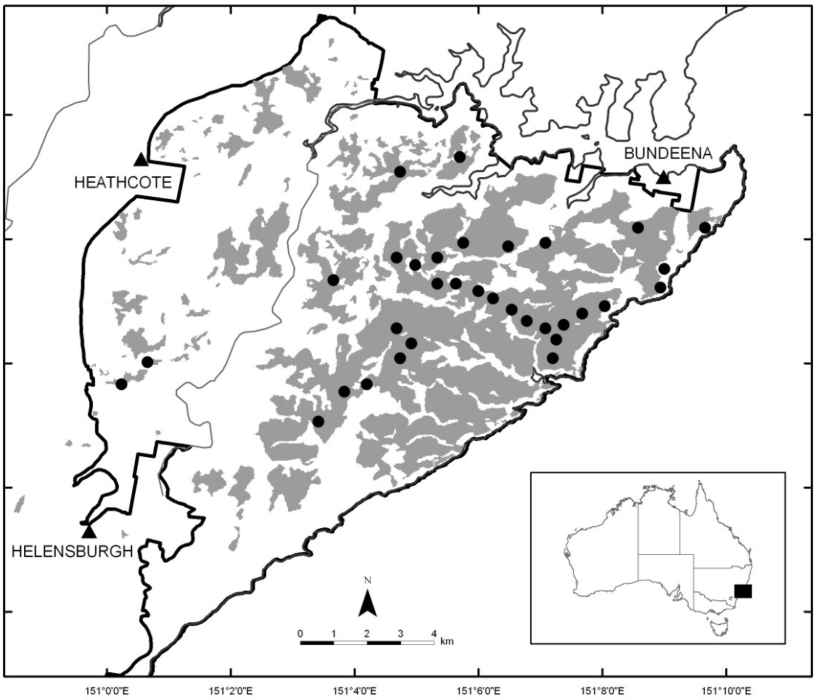

Figure 3. Map of the Royal National Park study area (Paper V) with 33 sampling sites marked with black dots. Coastal heath is shaded gray, the thick black line marks the border of Royal National Park, surrounded by the towns of Bundeena, Helensburgh and Heathcote marked with triangles.

The large herbivore I expected to have an effect on birds and small mammals differed among the studies. In Papers I, II, III and IV moose was the "treatment factor" in the system, while in Paper V I related small mammal captures to rusa deer and swamp wallaby.

Field procedures, lab procedures and statistical analysis

I live trapped small mammals for Papers I and V, while I used snap traps for Paper IV. More details about the trap types, spacing between traps and the type of baiting is found in the respective papers.

In the two studies on effects of moose on birds (Papers II and III), I provided nest boxes suitable for great tits and flycatchers. I monitored the nest boxes throughout the breeding season to determine nest box selection, starting date of egg laying, date of hatching, clutch size, number of hatchlings, fledglings and fledgling mass. For Paper III I also monitored parent feeding activity in the nests using activity loggers and cameras to record the type of prey delivered to the nest. Paper II contains bird data from two years, while Paper III contains bird data from five years.

The type of vegetation sampling differed among the studies. In Paper I, I did not survey the vegetation in the plots since this is a well documented study system, while in Papers II and III I recorded tree structure and canopy cover. For Paper IV I focused on the field layer vegetation and recorded height of bilberry (*Vaccinuim myrtillus*) and the percentage cover of species and groups of field layer species. In Paper V I recorded coverage of the main vegetation growth forms and estimated the vegetation structure i.e. percentage cover of vegetation in different strata. See the respective papers for more details.

For Paper III the sites were categorized according to forest vegetation types, and according to Norwegian forestry cutting classes. In Paper IV to reduce variation among sites I chose sites dominated by cowberry (*Vaccinium vitis-idaea*) or bilberry within two cutting classes.

In Papers II and III I recorded moose fecal pellets and browsing pressure, while in Paper V I recorded wallaby and deer fecal pellets. For Paper II I also collected arthropods from downy birch (*Betula pubescens*) branches, and in Paper IV I determined potential visibility to predators. See the respective papers for more details.

In Paper I I tested the preference of root vole for previously browsed bilberry in a cafeteria test. I presented the voles with bilberry clippings collected from the four simulated moose density treatments and recorded consumption by the voles. I also gained access to data on the chemical composition of bilberry from the four simulated moose densities.

In Paper IV I determined species, sex and age, and measured body length and mass of the trapped animals. For adult female voles I examined the uterus for placental scars or embryos (Alibhai 1982), as a measure of reproductive output. For Paper V I determined species of small mammal.

Statistical analysis

For all analyses I used the program R and associated packages (R Development Core Team 2011). Depending on the distribution of the response variable and whether random terms were appropriate or not I used general linear models, generalized linear models, general linear mixed models and generalized linear mixed models. For models with Poisson and binomial error structure I checked if there was overdispersion, and corrected for this if necessary. I used backward selection procedure if appropriate, with α set at 0.05. Again, more detailed description of the statistical analyses is given in the individual papers.

Results and discussion

In this thesis I describe complex interactions that were uncovered among large herbivores, vegetation, small mammals and birds, acting though food resources (Paper I), and through habitat structure (Papers II, III and IV) In Paper V the mechanisms are unknown, but most likely due to either changes in food resources or direct effect of trampling or predation.

Effects of cervids on food resources

Moose density affects vole preference for bilberry (Paper I)

In the cafeteria test, the voles consumed more bilberry from the high productivity compared to the low productivity sites. This agrees with previous reports that voles prefer plants growing at nutrient-rich sites (Danell et al. 1991). Although there were no main effects of simulated moose densities, I found a significant interaction between productivity of the site and simulated moose densities. At low productivity sites the voles preferred bilberry from the unbrowsed control treatment (0 moose per km^2), while they avoided plants from the 1 moose per km^2 density. At high productivity sites the preference pattern was reversed; voles avoided plants from the control treatment, while they preferred plants from the intermediate level of browsing (1 moose per km^2). This interaction indicated that plants at low and high productivity sites probably allocate resources differently as a response to the same level of browsing, and is predicted from the *growth differentiation balance hypothesis* (Herms & Mattson 1992; Stamp 2003). However, the voles did not show any particular preference or avoidance of the two highest levels of moose browsing (3 and 5 moose per km^2).

Although I found an effect of vole preference, I could not ascribe this to the differences in concentration of nitrogen, lignin or a range of secondary metabolites[4] in the plants. First, a lack of correlation between plant chemistry and browser selectivity is not uncommon in these types of studies (e.g. Hjätén et al. 1996). Second, some plant secondary metabolites have alternative functions in the plant, e.g. as protection against photodamage (Close & McArthur 2002), thus voles might not respond to levels of secondary metabolites induced by factors other than herbivory. I also expected voles to select large, fast growing nutrient rich shoots from tall bilberry, in accordance with the *plant vigor hypothesis* (Price 1991), but the results did not support this hypothesis.

Voles play a major role in the forest ecosystem and are affected at the population level by large scale changes in the nutritive quality of bilberry (Selås 2006). My results show that high moose densities have secondary effects through bilberry on small rodents,

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[4] Plant secondary metabolites are compounds not involved in growth, reproduction or development, but have other functions in the plant such as protection from e.g. herbivory or solar radiation.

and that these effects extend to vole species that are not bilberry specialists. Moose densities in Fennoscandia average around 1 moose per km^2 (Solberg et al. 2006), which is where I found an effect on vole preference. The current densities of moose could thus have a double effect on voles, first reducing the bilberry cover (Mathisen et al. 2010), and second reducing the palatability and possibly digestive value of bilberry at low productivity sites, but enhancing palatability and digestive value at high productivity sites. The crucial point is the productivity at a given site. Forestry (Panzacchi et al. 2010) and predation (Ims & Andreassen 2000) influence vole populations, but given that voles are controlled at least partly by their food resources (Oksanen et al. 1987; Dahlgren et al. 2007), I hypothesize that any factor influencing vole food sources over large geographical areas, such as moose browsing pressure could influence vole population dynamics.

Effects of cervids on habitat structure

Moose browsing reduces breeding success of great tits (Paper II)

In the first paper on great tit reproduction in relation to moose browsing I found that birch canopy cover was reduced, and number of tall trees lower at browsed compared to less browsed “control” plots. Moose browsing appears to reduce canopy cover of birch by not allowing young trees to escape browsing height. Moose browsing therefore reduces available leaf biomass for arthropods. However, I found no difference between “control” and browsed plots with regard to arthropod biomass on the branch scale. I interpret this as the total available arthropod biomass available to birds around the bird boxes is lower in browsed compared to control plots. I did not find any effects of browsing on numbers of eggs produced, number of hatchlings, date of hatching or fledgling mass. Hence, nestlings in browsed and control plots should get an even start in life and be of the same quality. Despite this, pairs in browsed plots produced on average 1.3 fewer nestlings compared to pairs on control plots. This suggests that moose browsing in this case had an effect only during the nestling season, reducing survival in the nest, presumably through lack of food. Van Balen (1973) found that number of fledglings decreases with decreased habitat quality. During the nestling period parent birds are restricted in their food search since they have to start their foraging trip from a central point. Models of central place foraging predicts that parent should optimize their prey delivery rate by minimizing travelling distances and selecting patches where the gain per unit cost is high (Naef-Daenzer 2000). Breeding pairs in browsed plots are “forced” to nest in areas where the gain per unit cost is lower and where traveling distance to good foraging patches is higher compared to pairs in control plots.

The browsing in the browsed plots was unnaturally high compared to natural browsing, however other studies have reported browsing levels approaching the levels of the browsed plots in this paper. Hence, the dynamics demonstrated here may be applicable to larger areas with naturally high browsing regimes.

Contrasting responses of passerines to moose browsing (Paper III)

In the second paper on bird reproduction in relation to moose browsing I found contrasting responses of flycatchers and great tits to moose browsing with regard to nest box selection, breeding success, fledgling weight and feeding activity.

Great tits increasingly preferred nest boxes further away from feeding stations as moose increased their use of feeding stations during the course of the study. Thus browsing effects accumulated over the five year study period, making the feeding stations less suitable for great tits, possibly by changing habitat structure and thus reducing foraging substrate or making the birds more prone to predation (McShea & Rappole 1997). Great tits also produced more fledglings further away from feeding stations, either as a consequence of less adult predation or better foraging substrates (McShea & Rappole 1997; Paper II).

Contrary to the great tits, flycatchers increased their preference for nest boxes close to feeding stations during the course of the study. This could be attributed to alleviated competition with great tits for nest boxes near the feeding stations. However, flycatchers also produced heavier fledglings and had higher feeding activity at feeding stations than elsewhere, which may be linked with nest box selection (Doligez et al. 2004). This pattern is more suggestive of preference rather than reduced competition with great tits.

Both species showed better reproductive performance in their preferred habitat. Flycatchers showed higher fledgling weights at high moose densities while great tits showed higher number of fledglings at low moose densities. Great tits may adjust clutch size to habitat quality (Dhondt et al. 1992). Great tits also showed a larger variation in fledgling production compared to flycatchers, indicating different life history strategies. Great tits may therefore respond to high moose browsing by reducing the number of fledglings while flycatchers respond by increasing fledgling weight. Feeding rates also corresponded to the preferred habitat of the respective species. Great tits had highest feeding rates where they produced most fledglings and flycatchers where they produced the heaviest fledglings. These results support the hypothesis that food availability through reduced foraging substrate is the mechanism driving differences in breeding success between high and low moose browsing for both species (Paper II). Alternatively, moose browsing could cause increased production of defensive compounds in for example birch, affecting insect herbivores in a similar matter to voles in Paper I, causing a reduced abundance of herbivorous arthropods. Great tits could then be responding to this indirect effect of induced plant defense by producing fewer fledglings. However, as I argue in Paper II, arthropod abundance at the branch scale did not differ between browsed and control plots, hence, moose browsing is not causing qualitative changes in leafs that arthropod abundance is responding to.

The two bird species responded quite differently to moose browsing. Great tits prefer caterpillars (Nour et al. 1998) and forage on leaves, and may thus be more susceptible to reduced birch leaf biomass caused by moose browsing (Paper II). Flycatchers on the other hand have a more diverse diet, forage in the air and on the ground (Sanz 1998), and may thus perform better in the more open habitat in heavily browsed areas. Hence, moose browsing have different effects on two relatively similar passerine bird species through changing habitat structure and foraging substrate for these insectivorous birds.

Small mammal responses to moose feeding stations (Paper IV)

Field layer vegetation at feeding stations had a much higher cover of grasses and nutrient-demanding forbs than at sites further away, and this change in habitat structure had consequences for the captures of small mammals. Captures of *Microtus* spp. and common shrews decreased as distance from feeding stations increased, while captures of bank voles increased as distance from feeding stations increased, however this effect was not statistically significant. These responses are coupled with the known habitat preferences of these species, with *Microtus* spp. and shrews preferring productive grasslands (Hanski & Kaikusalo 1989; Panzacchi et al. 2010) where their main food plants and invertebrate abundances are higher. Despite effects on the numbers of captures I did not find any effect of distance from feeding stations on reproductive success on any of the vole species, thus either survival or immigration must be higher in the preferred habitat of the respective species. Also, I found no effect of distance to feeding station on total small mammal biomass. The reason could be that numbers of *Microtus* spp. and shrews and thereby biomass decreased with increasing distance from feeding stations, while simultaneously, bank vole numbers and thereby biomass increased (non-significantly) with distance from feeding stations. Finally, the inter-annual range in small mammal biomass and inter-annual range in number of small mammal captures was not affected by distance to feeding stations. Thus, moose feeding stations do not seem to function as sites of high winter survival for small mammals, and do not support higher densities of small mammal predators. However, a complete rodent cycle is needed to draw firm conclusions on this issue. I am fairly confident that the results in this paper are due to changed habitat structure, as not only the architecture of the plants (Papers II and III), but also the plant species composition was altered, changing the habitat from dwarf shrub dominated to grass and forb dominated. Although these changes affect both food sources and habitat structure, the main change is altered habitat structure. Bank voles were not heavily affected by moose feeding stations, but feeding stations may be important for *Microtus* spp. and shrews as they provide islands of preferred habitat that allow these small mammals to penetrate into the matrix of less preferred forest habitat.

Relationship between small mammals and large herbivores in coastal heath (Paper V)

The general pattern in this study was that there were fewer captures of small mammals in sites currently occupied by deer compared to sites without deer. For brown antechinus, bush rats and New Holland mice, this effect was statistically significant, although not for swamp rats. These negative patterns found here is in accordance with other studies on small mammal abundance in relation to large herbivores (Keesing 1998; Saetnan & Skarpe 2006; Johnston & Anthony 2008; Buesching et al. 2011). Captures of bush rats were negatively and New Holland mice positively related to historical deer habitat use. Brown antechinus and swamp rats were, however, not affected. I found no relationship between current wallaby habitat use and captures of any of the small mammals, suggesting a lower impact of wallabies compared to deer. Similar to the pattern for the historical presence of deer, I found a negative relationship between historical wallaby habitat use and captures of bush rats and a positive relationship with captures of New Holland mice. Despite these relationships, I was unable to confirm any of the effects of the large herbivores as being due to changes in habitat structure for the small mammals. I speculate that the deer might be causing direct effects rather than indirect effects on the small mammals through trampling (Beintema & Muskens 1987; Pakanen et al. 2011) or possibly predation (Pietz & Granfors 2000; Ellis-Felege et al. 2008). Alternatively, the results might reflect qualitative rather than quantitative changes in vegetation (Paper I).

Interestingly, the insectivorous common shrew (Paper IV) and the insectivorous pied flycatcher (Paper III), which both feed on ground invertebrates showed the same habitat preference pattern with respect to distance from feeding stations and moose abundance. However, the insectivorous brown antechinus in coastal heath (Paper V) was affected negatively by current deer abundance. This discrepancy may be due to deer abundance in coastal heath not increasing productivity of the site in the same way that moose feeding stations do. In low productive environments herbivory may decrease nutrient cycling and reduce productivity (Pastor et al. 2006), which again may reduce arthropod abundance. Alternatively, it could arise due to the above mentioned changes in vegetation quality as a plant response to herbivory, or a direct negative effect of deer, while moose browsing and moose feeding stations had positive effects on the insectivores by increasing arthropod abundance.

General discussion

Productivity of a system may modulate the effect of herbivory on plant responses exemplified by the growth differentiation balance hypothesis (Herms & Mattson 1992;

Stamp 2003), and I have shown through this thesis that productivity affects the direction and strength of bird and small mammal responses to cervids (Papers I, II, III and IV).

In an experimental study with large herbivore exclosures along a productivity gradient, Pringle et al. (2007) found that ungulates reduced the abundance of insectivorous lizards by reducing both tree density (habitat availability) and beetle density (food availability). Thus, they incorporate and disentangle the effects of the two proposed mechanisms addressed in this thesis. In addition, they showed that the effects of the large herbivores increased with decreasing productivity, meaning that the highest effect was found in sites with the lowest productivity. This implies that effects of large herbivores on the abundance of lizards, trees and beetles in control plots were reduced with increasing productivity, or that the density in browsed plots increased with productivity, or a combination of the two. It is likely that abundance of birds and small mammals also would respond to an interaction between productivity and large herbivore abundance. This has to my knowledge not been investigated in a proper experimental gradient setting. However, Cheng & Ritchie (2006) found that simulated livestock grazing caused reduced individual growth rate, higher foraging time and reduced apparent vigilance in juvenile Utah prairie dogs (*Cynomys parvidens*) in a low productivity environment. Cheng and Ritchie (2006) contrasts this to a facilitative effect of cattle found in a high productivity habitat on black-tailed prairie dogs (*Cynomys ludovicianus*) (Krueger 1986), effects that may have consequences for the abundance of prairie dogs.

I find stronger effects of the introduced rusa deer compared to the native wallaby (Paper V), probably due to their higher density (Moriarty 2004b) and body mass (Menkhorst & Knight 2004). Some authors have pointed out the devastating effects of introduced deer on biodiversity (Dolman & Waber 2008; Spear & Chown 2009). However, it may be more sensible to avoid the “native good, alien bad” maxim that often has dominated the literature (Goodenough 2010), and adapt a more balanced view of alien species. Alien species may have detrimental effects on native species, but they may simultaneously have positive effects on other species, and these positive facilitating effects needs also to be considered. Despite this, I think that as a general rule the threshold for initiating actions against alien species should be lower compared to native species (Nugent et al. 2011), and that the management actions can be tougher.

I think that the severity of the impacts of cervids on the ecosystem is better described by their density than their geographic origin. All the papers in this thesis illustrate the importance of cervid density, and some of them illustrate that impacts are not just a matter of presence or absence (Papers I, III, IV and V). There are density thresholds where negative effects may occur. The impacts of increasing density are not likely to be linear, but rather to be of little importance up to a threshold (or rather threshold continuums) where the impacts become more prominent (Putman et al. 2011). The threshold of impacts on ecosystems varies depending on the habitat, and it varies depending on what species are considered within that habitat as some species are negatively, and other are positively affected by increasing cervid densities (Papers III, IV and V). If we focus on biodiversity in general rather than single species, the *intermediate disturbance hypothesis* predicts that species diversity has a unimodal relationship with disturbance (Connell 1978). We may consider cervids as a disturbing factor to the system and thus predict that as cervid density increases, diversity will first increase and then reach a tipping point after which it is reduced (Figure 4). As previously mentioned, we may expect an interaction between cervid densities and site productivity. I expect the unimodal relationship between cervid density and species richness to be steeper in low productivity habitats, while less steep in high productivity habitats (Figure 4). Also, I propose that the maximum cervid density where species are present would increase as productivity increases (Figure 4).

This relationship between gradients of cervid density and species richness has been found for invertebrate (beetle) species richness (Melis et al. 2006b). However, it has not been shown for species richness of birds which shows a generally negative response to increasing deer densities (Allombert et al. 2005b; Mathisen & Skarpe 2011). Small mammal species richness have been shown to be unaffected by a gradient in deer densities (Moseley et al. 2011). The reasons for the discrepancy between invertebrates, birds and small mammals are unclear. The study of Mathisen and Skarpe (2011)[5] and Moseley et al. (2011)[6] could be to the right of the tipping point in figure 4 and we thus should expect a decrease in diversity, which Mathisen and Skarpe (2011) show, but not Moseley et al (2011). Allombert et al. (2005b) have study islands along the whole cervid

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[5] Conducted in the same system as Papers II, III and IV.

[6] Moseley et al. (2011) investigated three densities of deer (12, 31 and 50 per km^2)

density gradient. They find that the species assemblage changes with increasing deer density, where gamma diversity[7] is stable and alpha diversity decreases.

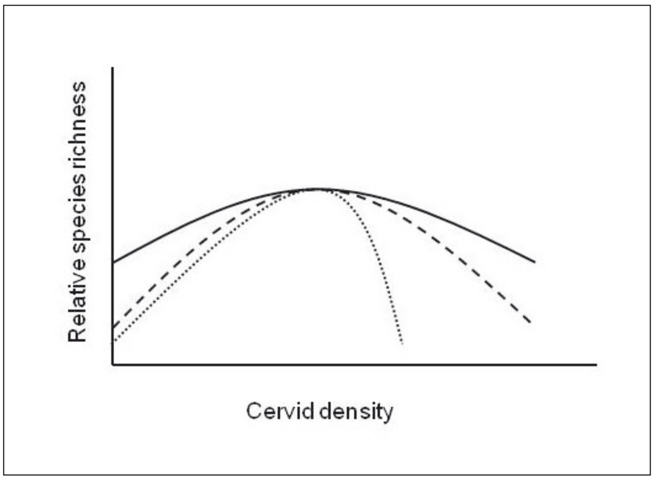

Figure 4. The intermediate disturbance hypothesis, adopted for cervid densities under varying site productivity. Dotted line denotes low productivity, broken line denotes intermediate productivity while unbroken line denotes high productivity. Relative species richness means that species richness is standardized among productivity levels. (Modified from Connell 1978).

In addition to and interwoven with the indirect effects wrought by herbivory, cervids may also affect small mammal and bird habitats through other effects such as trampling of vegetation, wallowing, antler rubbing and addition of dung and urine (Gill 2006; Hobbs 2006). Addition of dung and urine generally increases nutrient loading and cycling, and although the effects are small averaged over the total area of habitat used by the large herbivore, they may be substantial if the herbivores concentrate at focal sites (Pastor et al. 2006). From calculations in South African non-cervid multispecies assemblages trampling effects on vegetation may be substantial, with 15 – 25 % area trampled of total area used by an individual per year (Hobbs 2006). These calculations are sensitive to the assumptions they are based on as the area trampled is scaled up spatially and temporally. Nonetheless, trampling may have a large impact on the vegetation and concurrently small mammals and birds that utilize this vegetation, especially if the

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[7] Alpha diversity in this case refers to species richness within a sampling plot, while gamma diversity refers to species richness within an island (Allombert et al. 2005b).

trampling is concentrated at sites of high cervid activity (papers II, III and IV). Trampling may also cause direct negative effects on small mammals and birds (Beintema & Muskens 1987; Flowerdew & Ellwood 2001; Pakanen et al. 2011). Trampling may be important for small mammals hibernating or birds nesting on the ground. Not much evidence exists from wild cervids, but there are profound effects of trampling of bird nests in grazing systems with livestock (Beintema & Muskens 1987; Pakanen et al. 2011). Although the stocking densities of livestock are much higher compared to the density of most wild cervids, trampling by cervids may pose an additional strain on birds and small mammals. Another, direct negative effect of large herbivores is predation. It is rarely considered as an impact of large herbivores, and is most evident for omnivores such as the wild boar (*Sus scrofa*) (Suominen & Danell 2006), but other species such as white-tailed deer may also depredate birds (Pietz & Granfors 2000; Ellis-Felege et al. 2008) and possibly small mammals if they encounter them. However, detecting a predation event does not imply a population effect and its extent and importance on small mammal and bird populations is largely unknown.

Management implications

None of the Scandinavian birds or small mammals are considered threatened species in Norway (www.artsdatabanken.no, accessed September 26th 2011). They may however serve as models for predicting effects of cervids on endangered species with similar habitat preferences, although care should be taken when generalizing, exemplified by the contrasting effects of the great tit and pied flycatcher (Paper III). In Australia the situation with the endemic species is a bit different. Bush rats and brown antechinus are not considered threatened (www.iucnredlist.org, accessed September 26th 2011). Swamp rats are currently classified as of least concern, but their population trend is negative. The threats are coastal development, and “inappropriate burning regimes” resulting in habitat changes (www.iucnredlist.org, accessed September 26th 2011). Fortunately, swamp rats are affected by neither rusa deer nor swamp wallabies. New Holland mice are considered vulnerable, facing a high risk of extinction in the wild with a decreasing population trend (www.iucnredlist.org, accessed September 26th 2011). Managing New Holland mice through rusa deer would be challenging as this species is related negatively to current deer habitat use, but related positively to historical habitat use (Paper V). I would rather manage it through prescribed burns, as it is an early successional fire-adapted species (e.g Fox 1982). As shown in Paper I, moose densities may cause changes in the food plants for voles, and I hypothesize that moose browsing pressure could potentially affect vole population dynamics. If this is the case, moose could be the cause of voles not reaching the densities experienced in former years (Hanski et al. 1993; Hörnfeldt 2004), which would have large implications for the boreal food web.

In this thesis I have shown that cervids have an impact on birds and small mammals, and that responses vary. Hence, it is impossible to classify cervids as either "good" or "bad", as illustrated by Figure 4. Managers need to find the appropriate balance of cervid densities, not too many and not too few by for example assessing their impacts on assemblages of indicator plants (Williams et al. 2000). The challenge is to establish a consensus on what those densities should be.

Future prospects

In this thesis I have discovered that large herbivores have both positive and negative effects on abundance and reproduction of small mammals and birds. Since these animals are important as prey, the next step would be to include the next trophic level, predators (McCauley et al. 2006), and test what effects large herbivores may have on predators of small mammals and birds. In paper IV I hypothesize that moose feeding stations function as small predator feeding stations, I did not find this, but it should be tested over a complete rodent cycle.

Although we have knowledge of the effects of moose feeding stations on arboreal arthropods (Paper II), the effect of moose feeding stations on invertebrates inhabiting other vegetation strata needs to be tested more explicitly. Specifically, investigations are needed into the effects of feeding stations on ground dwelling invertebrates that probably are important as prey to shrews and flycatchers, and also on flying insects that are important to flycatchers.

In Paper V I have discovered that small mammals generally are negatively related to deer habitat use. Deer in Australia are recognized as pests in some states and territories (Hall & Gill 2005), despite this there seems to be an disproportionally large gap between the large focus on introduced deer in Australia and the limited knowledge of their impacts on vegetation, invertebrates, small mammals, birds and native large herbivores, a point also emphasized by Nugent et al. (2011). These are areas that need further attention, preferably though replicated experimental gradient studies, with reliable estimates of deer densities (Putman et al. 2011).

Flowerdew and Ellwood (2001) suggested a decade ago that replicated exclosure studies provide a way of better understanding the mechanisms of how cervids affect other taxa. Nonetheless, studies on this topic are still conducted using non-experimental approaches, including, ironically, parts of this thesis. I think the reasons for this are that experimental studies are costly and they also need to run for a longer period than the normal research project or PhD before they start to yield trustworthy results. However, one needs to consider how to achieve this, i.e. by initiating and funding more long-term studies with an experimental approach, and sustaining funding for already established experiments.

Acknowledgements

I would like to thank Harry P. Andreassen, Christina Skarpe, Eivin Røskaft, Hans C. Pedersen, Chris R. Dickman and Erlend B. Nilsen for valuable comments on this synthesis.

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Paper I

Changes made to the following proof of Paper I

Page 344, Second column, the second sentence in the second paragraph under ”Simulated moose browsing” reads “The chosen densities are…”, but should read “The chosen densities were…”

Page 345, Second column, line 6-7 in the first paragraph under “Chemical analysis and morphology” reads “The bilberry was dried (at 22 ° C, relative humidity 10%)”, but should be: “The bilberry was dried (at 22 ° C, 10 % relative humidity)”

Page 346, First column, 17th line under “Data analysis” reads: “The site productivity index for the sites ranged from 1.2 to 6.8 and was for this analysis grouped in 2 categories: below and above a productivity index of 5; and high productivity (3 sites) and low productivity(5 sites)”, here the underlined “and” has been deleted.

Page 347, First column, lines 1-4: “When testing for an effect of productivity and moose density on deviance, we did not find any effect of productivity, due to productivity summing up to 1 in every batch (Table 3), or moose density (Table 3).”

This should be:

“When testing for an effect of productivity and moose density on deviance, neither did we find any effect of productivity, due to deviance summing up to 0 in every batch (Table 3), nor moose density (Table 3).”

Figure 1: Values on the Y-axis in the proof are -0.10; -0.050; .00; 0.05; 0.10; 0.15, but should be:

-0.10; -0.05; 0.00; 0.05; 0.10; 0.15

Is not included due to copyright

Paper II

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Paper III

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.

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. 2005a; 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. 2005b; 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^{o}N, 11^{o}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 ^{o}C (May – September) and mean winter temperature of -5.8 ^{o}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 % (± 6 SE) of the boxes were empty each year.

Great tits produced on average 7.52 (±1.05) fledgings at far distance from feeding stations, and 1.15 (±1.09) fledglings less at feeding stations than at far distance, and 1.02 (±1.09) fledglings less at intermediate sites than at far distance (Table 1). Pied flycatchers produced on average 5.1 (±1.1) fledgings at far distance, and 1.2 (±1.1) more fledgings at feeding stations, and 1.1 (±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.

Acknowledgements

This study was funded by Hedmark University College and the Norwegian Research Council. We are grateful to the landowners and the landowner association in Stor-Elvdal municipality and especially Knut Nicolaysen, for support, providing information about moose feeding and giving us permission to put up nest boxes. Thanks go to the numerous students that have been a great help in the field. Thanks to Harry Andreassen, for help with planning this study, to Tom Hætta for going through the video films, to Kjell Danell for helpful comments on the manuscript, to Tore Slagsvold for advice on filming of nest boxes and bird ecology, and to Jos Milner for language corrections. Thanks also to Anders Lamberg for building the nest box loggers, and to Stephen Parfitt for maintaining them.

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Tables

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	2.02	0.05	38.34	<0.001
	FS	-0.14	0.08	1.70	0.089
	INT	-0.02	0.08	0.29	0.769
	Chi square test of distance to feeding station: $\chi^2_{2,73}$=3.12, p = 0.210				
Pied flycatcher	FAR	1.64	0.08	19.98	<0.001
	FS	0.15	0.10	1.49	0.136
	INT	0.06	0.11	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	15.50	0.65	612	23.62	<.001
	FS	-0.29	0.43	64	0.67	0.504
	INT	-0.20	0.42	64	0.48	0.631
	2005	2.49	0.68	15	3.68	0.002
	2006	2.27	0.70	15	3.23	0.006
	2007	2.38	0.58	15	4.09	0.001
Pied flycatcher	FAR	14.0	0.26	424	53.10	<.001
	FS	0.49	0.27	53	1.85	0.071
	INT	0.69	0.26	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	0.13	0.19	11	0.72	0.485
	Day	0.17	0.02	218	8.45	<.001
	Day^2	-0.0053	0.0008	218	6.42	<.001
	Hatchlings	0.067	0.063	11	1.07	0.307
	FS*day	-0.020	0.010	218	1.95	0.052
Pied flycatcher						
	FAR	4.21	0.27	157	15.80	<.001
	FS	-0.14	0.17	8	0.83	0.429
	Day	0.30	0.03	157	11.35	<.001
	Day^2	-0.0168	0.0014	157	11.71	<.001
	Hatchlings	0.143	0.041	8	3.51	0.008
	FS*day	0.027	0.014	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 ± 5.7	19.8 ± 6.7	33.4 ± 3.6	$\chi^2_{2,31}$=37.55	0.120
Prey item volume all groups	0.37 ± 0.08	0.20 ± 0.06	0.41 ± 0.08	$F_{2,33} = 0.56$	0.574
Larvae volume Lepidoptera	0.37 ± 0.10	0.15 ± 0.03	0.28 ± 0.03	$F_{2,26} = 1.37$	0.271
Imago Coleoptera	0.15 ± 0.05	0.16 ± 0.02	0.15 ± 0.05	$\chi^2_{2,31} = 1.10$	0.577
Imago Diptera	0.04 ± 0.02	0.02 ± 0.01	0.06 ± 0.04	$\chi^2_{2,31} = 0.55$	0.759
Imago Hymenoptera	0.10 ± 0.07	0.06 ± 0.04	0.06 ± 0.02	$\chi^2_{2,31} = 0.39$	0.823
Imago Lepidoptera	0.08 ± 0.03	0.02 ± 0.01	0.06 ± 0.01	$\chi^2_{2,31} = 7.84$	**0.020**
Larvae Coleoptera	0.04 ± 0.02	0.08 ± 0.03	0.06 ± 0.01	$\chi^2_{2,31} = 1.04$	0.595
Larvae Diptera	0.00	0.00	0.02 ± 0.02	$\chi^2_{2,31} = 7.82$	**0.020**
Larvae Hymenoptera	0.08 ± 0.03	0.19 ± 0.10	0.11 ± 0.04	$\chi^2_{2,31}= 3.71$	0.157
Larvae Lepidoptera	0.36 ± 0.09	0.31 ± 0.12	0.38 ± 0.07	$\chi^2_{2,31}= 1.45$	0.458
Aranea	0.15 ± 0.06	0.16 ± 0.07	0.12 ± 0.02	$\chi^2_{2,31} = 0.86$	0.650
Larvae / Imago ratio all groups	2.17 ± 0.79	2.25 ± 0.45	3.12 ± 0.62	$\chi^2_{2,31}= 2.13$	0.344

Figures

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).

Fig. 2 Nest-box occupation (occupied/available nest boxes) 2004-2008 by great tits (above) and pied flycatchers (below) at feeding stations for moose (FS), intermediate distance (INT: 50-500m) and FAR from feeding stations (> 500 m).

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).

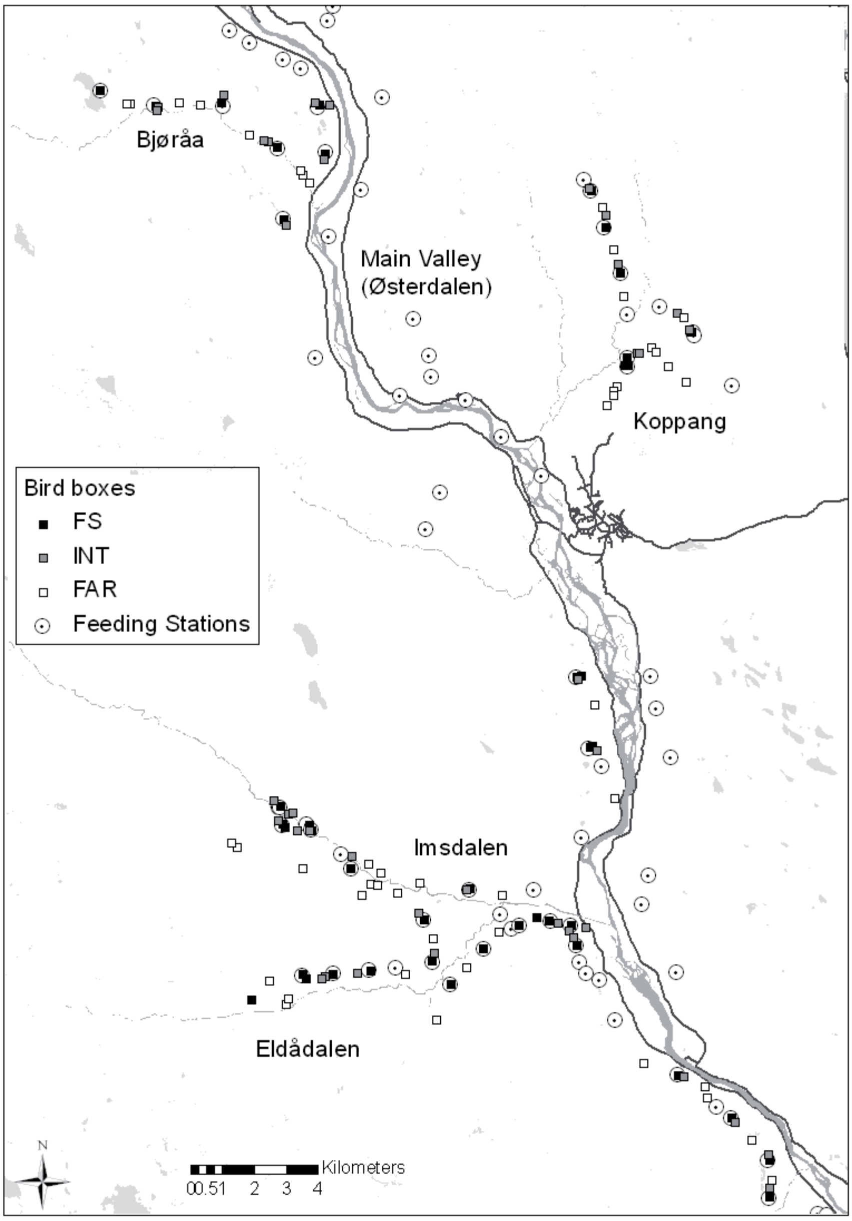
Bjøråa
Main Valley
(Østerdalen)
Koppang
Bird boxes
■ FS
▨ INT
□ FAR
⊙ Feeding Stations
Imsdalen
Eldådalen
N
Kilometers
0 0.5 1 2 3 4

Fig 1.

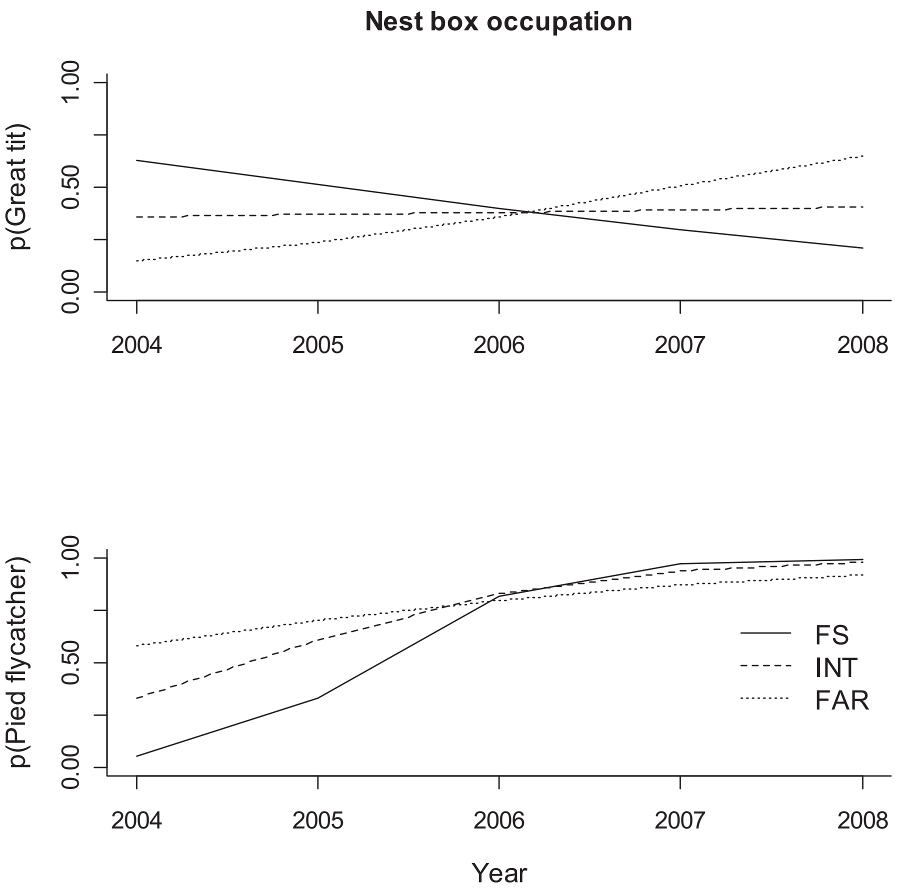
Nest box occupation
p(Great tit)
0.00
0.50
1.00
2004
2005
2006
2007
2008
p(Pied flycatcher)
0.00
0.50
1.00
FS
INT
FAR
2004
2005
2006
2007
2008
Year

Fig. 2

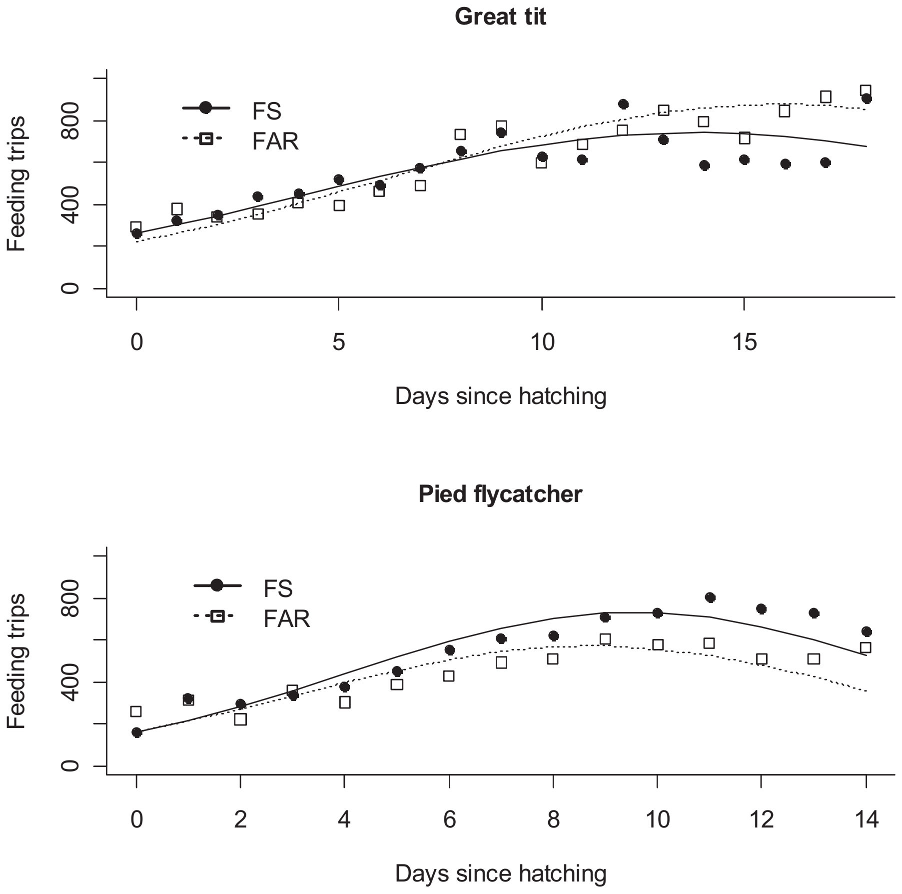
Great tit
Feeding trips
0
400
800
FS
FAR
0
5
10
15
Days since hatching
Pied flycatcher
Feeding trips
0
400
800
FS
FAR
0
2
4
6
8
10
12
14
Days since hatching

Fig 3.

Supplementary material for: Contrasting responses of two passerine bird species to moose browsing. European Journal of Wildlife Research. Mathisen K. M, Pedersen, S., Nilsen, E. B and Skarpe C.

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	0.36 ± 0.09	0.01 ± < 0.00	0.01 ± < 0.00	FS/Int/Far	$X^2{}_2 = 129.95$, $p <.001$
2006	0.73 ± 0.09	0.05 ± 0.01	0.02 ± < 0.00	Year	$X^2{}_2=1589$, $p <.001$
2007	0.32 ± 0.05	0.02 ± < 0.00	0.01 ± < 0.00	FSIntFar*year	$X^2{}_4 =7.53$, $p = 0.110$
Birch browsing (%)					
2004	78.2 ± 2.2	37.8 ± 5.6	13.3 ± 4.8	FS/Int/Far	$X^2{}_2 = 62.08$, $p <.001$
2006	80.7 ± 3.9	61.3 ± 4.8	47.5 ± 8.8	Year	$X^2{}_2 = 2725$, $p <.001$
2007	97.0 ± 0.9	81.0 ± 3.6	77.1 ± 3.4	FSIntFar*year	$X^2{}_4 = 125.7$, $p <.001$
Pine browsing (%)					
2004	83.3 ± < 0.00	58.7 ± 7.5	61.1 ± 13.6	FS/Int/Far	$X^2{}_2 = 4.78$, $p = 0.092$
2006	69.2 ± 3.9	59.8 ± 4.6	42.8 ± 17.6	Year	$X^2{}_2 =1570$, $p <.001$
2007	96.1 ± 2.0	91.3 ± 2.6	90.3 ± 2.8	FSIntFar*year	$X^2{}_4 = 71.20$, $p <.001$
Spruce browsing (%)					
2004	23.1 ± 7.6	1.92 ± 1.3	0.00 ± < 0.00	FS/Int/Far	$X^2{}_2 = 5487$, $p <.001$
2006	53.4 ± 4.8	17.4 ± 3.3	4.50 ± 2.1	Year	$X^2{}_2 =1483$, $p <.001$
2007	68.0 ± 5.4	29.1 ± 4.9	8.10 ± 1.5	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	8.2 ± 1.7	10.1 ± 1.8	12.7 ± 2.2	$F_{2,125} = 1.09$	0.341
Pine < 3m height	0.6 ± 0.1	0.9 ± 0.13	1.1 ± 0.2	$F_{2,125} = 3.86$	0.024
Spruce > 3m height	10.6 ± 2.5	8.7 ± 1.6	8.7 ± 1.4	$F_{2,125} = 0.04$	0.960
Spruce < 3m height	4.4 ± 0.7	3.1 ± 0.4	3.6 ± 0.58	$F_{2,125} = 0.56$	0.574
Birch > 3m height	9.7 ± 1.5	21.6 ± 3.5	9.1 ± 1.1	$F_{2,125} = 8.15$	<.001
Birch < 3m height	10.1 ± 1.7	6.9 ± 1.0	9.5 ± 1.5	$F_{2,125} = 1.60$	0.206
RSA > 3m height	2.5 ± 1.9	0.4 ± 0.2	0.5 ± 0.4	$F_{2,125} = 1.20$	0.306
RSA < 3m height	3.0 ± 0.6	2.5 ± 0.8	1.8 ± 0.4	$F_{2,125} = 1.19$	0.308
Field layer vegetation cover(%)					
Lichens	16.9 ± 2.4	23.5 ± 3.1	22.8 ± 2.5	$F_{2,125} = 2.52$	0.085
Herbs and grasses	34.8 ± 4.6	14.1 ± 3.1	13.4 ± 3.3	$F_{2,125} = 10.55$	<.001
Dwarfshrubs	37.6 ± 3.6	52.9 ± 3.6	53.0 ± 3.9	$F_{2,125} = 5.36$	0.006
Elevation	482 ± 21	454 ± 17	486 ± 20	$F_{2,125} = 0.17$	0.843

Paper IV

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Paper V

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*

1994 Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994 Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995 Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors

1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis

1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems

2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar

2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004 Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004 Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004 Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004 Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004 Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004 Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005 Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005 Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005 Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005 Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005 Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005 Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005 Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005 Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005 Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005 Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005 Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005 Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005 Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease

2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*

2011 Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011 Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011 Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011 Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011 Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011 Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011 Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011 AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011 Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011 Kari Bjørneraas	ph.d Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011 John Odden	ph.d Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep