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Effects of power lines on moose (*Alces alces*) habitat selection, movements and feeding activity

Thesis for the degree of Philosophiae Doctor

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CONTENTS

PAPER I-IV

LIST OF PAPERS

This thesis is based on the following papers:

Bartzke, G., R. May, S. Stokke, E. Røskaft, and S. Engen. in press. "*Comparative effects of power lines and roads on moose (Alces alces) habitat selection*." *in* Proceedings of the Environmental Concerns in Rights-of-Way Management: 10th International Symposium. Phoenix, Arizona, USA.[1]

Bartzke, G.S., R. May, E. Røskaft. "Differential barrier and corridor effects of power lines, roads and rivers on moose (*Alces alces*) movements." *Manuscript*[2]

Bartzke, G.S., R. May, H. O'Neill, S. Rochelle, S. Stokke. "Edge effects at a high-voltage power line on moose (*Alces alces*) browsing and habitat use." *Manuscript*[3]

Bartzke, G.S., R. May, K. Bevanger K., S. Stokke S., E. Røskaft. "A review on the effects of power lines on ungulates and its implications for power line routing and rights-of-way management." *Manuscript*[4]

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[1] I conducted the analysis with the help of R. May and S. Engen and wrote the manuscript with advice from all co-authors. E. J. Solberg and C. M. Rolandsen had the initial idea and provided the data. All contributed ideas and helped with the interpretation of the results.

[2] The initial idea emerged from the first manuscript. I performed the analyses with the help of R. May and wrote the manuscript with input from of all co-authors. E. J. Solberg and C. M. Rolandsen provided the data. All contributed ideas and helped with the interpretation of the results.

[3] R. May, S. Stokke, E. J. Solberg, C. M. Rolandsen and I developed the idea and planning of the study. I performed the analyses and wrote the manuscript with advice from R. May and S. Stokke. All contributed ideas, to the collection of the data and helped with the interpretation of the results.

[4] I conducted the review, GIS analysis and wrote the manuscript with contributions from R. May and advice from all co-authors. All contributed ideas and helped with the interpretation of the results.

INTRODUCTION

Power lines as sources of habitat loss and fragmentation

Human population growth and industrialization have resulted in an expansion of transportation infrastructure (Canning 1998) that encroaches and fragments wildlife habitats (Rosselli 2002, Nellemann et al. 2003, Jędrzejewski et al. 2004, May et al. 2006). Linear features like power lines and roads may particularly affect habitats that would otherwise be spared from other human developments (Byron et al. 2000, Nellemann et al. 2001, Goosem 2007). In Norway (**Figure 1**), energy production and transport as well as road construction were the main causes for the reduction of areas more than one km from major infrastructure developments by four percent within ten years (1998 - 2008) (Norwegian Environment Agency 2013).

Nearly 200,000 km overhead power lines exist in Norway, of which approximately nine percent carry voltages of 132 kV and above (Statistics Norway 2011). In total, there are approximately as many public (Brunvoll and Monsrud 2013), private (Norwegian Mapping Authority 2012) and forest (Statistics Norway 2013b) roads. The Norwegian central grid power line operator Statnett is planning to increase the construction of new power lines to over 300 km per year until 2020 (Statnett SF 2013) to satisfy the increasing demand for electric energy and to provide distribution facilities for an increased production of renewable energies.

A reduction of habitat supports fewer individuals, exemplified by declining relative abundances of mammals in forest fragments of decreasing size (Chiarello 2000, Crooks 2002, Michalski and Peres 2007). Species numbers are predicted to decline with the reduction of area and increasing isolation of areas according to the theory of island biogeography (MacArthur and Wilson 1967). Power line rights-of-way (ROWs), cleared areas under power lines, reduce forest area and separate remaining forest patches. In fragmented landscapes, the persistence metapopulations can further be influenced by the dynamics of local populations, patch quality and connectivity (Ovaskainen and Hanski 2003, Summers et al. 2011). Power line ROWs may alter these parameters through the provisioning or removal of resources, edge and barrier effects.

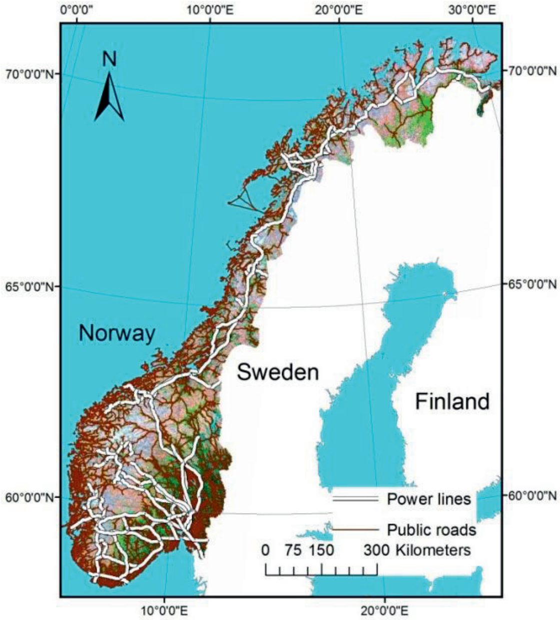

Figure 1 Map showing central power line (thick white lines) and public road (thin brown lines) grid in Norway. Green areas depict forests.

Wildlife responses to power line ROWs

Some species that prefer canopy cover used power line ROWs less than forest (birds: Kroodsma (1982b), Rosselli (2002); small mammals: Doucet and Brown (1997), Clarke et al. (2007), Storm and Choate (2012); ungulates: Joyal et al. (1984), Rieucau et al. (2007)), and animal observations declined after the construction of a power line ROW (birds: Anderson (1979)) or similar clearings (birds and small mammals: Doucet and Bider (1984)).

However, early to mid-successional habitats develop after the clearing of forest (Bramble and Byrnes 1982) (**Figure 2**). Those can attract species favoring open habitats (birds: Anderson et al. (1977), Kroodsma (1982a), Bramble et al. (1984), Bramble et al. (1986); reptiles: Doucet and Bider (1984), Yahner et al. (2001b); amphibians: Yahner et al. (2001b); insects: Russell et al. (2005); small mammals: Bramble et al. (1992), Clarke et al. (2007), Storm and Choate (2012)), resulting in an increased abundance (birds: Anderson (1979)). Some ungulates foraged more in power line ROWs compared to forest (Bramble and Byrnes 1972, Lamothe and Dupuy 1984, Ricard and Doucet 1999).

Figure 2 Power line ROW traversing a forest in central Norway. The open corridor is bordered by forest edges.

Power line ROWs with intermediate levels of succession may even support more species than surrounding mature forest, because both colonizers and climax species should able to co-exist according to the intermediate disturbance hypothesis (Connell 1978). This is supported by increased species richness in early to mid-successional power line ROWs compared to forests (birds: Anderson (1979), Wunderle Jr et al. (1987), Yahner et al. (2002); small mammals: Johnson et al. (1979), Bramble et al. (1992); arthropods: Ditsworth et al. (1982)).

Similarly, more species may be found along forest edges that bridge open ROW and forest habitat (birds: Yahner et al. (2002), Kroodsma (1982b)), as for other types of forest edges (small mammals: Menzel et al. (1999)). Not all studies support this theory (birds: Kroodsma (1984, 1987); small mammals: Johnson et al. (1979), Fortin and Doucet (2008)), and increased species richness does not always coincide with increased biodiversity (Anderson 1979, Ditsworth et al. 1982). Power line ROWs, similar to roads (DeMers 1993, Niemelä and Spence 1999, Brown et al. 2006), may facilitate the spread of generalist or invasive species (Goosem and Turton 2006, Clarke et al. 2007, Arner et al. 2008). This could result in reduced evenness (Johnson et al. 1979).

Effects on forest ungulates

Ungulates could be affected differentially by power lines through the removal of forest cover, alterations of forage availability in rights-of-way as well as disturbance through the physical structure, corona noise (Flydal et al. 2010) or electromagnetic fields (Burda et al. 2009) (**Figure 3**). Reindeer (*Rangifer tarandus tarandus*) in Norway were suspected to associate power lines with danger (Vistnes et al. 2004) and to avoid areas in the proximity of power lines (Vistnes and Nellemann 2001). This could result in a functional loss of habitat (Polfus et al. 2011). If ungulates perceive power lines as a potential risk, they should become more vigilant and forage less and in their proximity according to the risk-allocation hypothesis (Lima and Bednekoff 1999, Frid and Dill 2002).

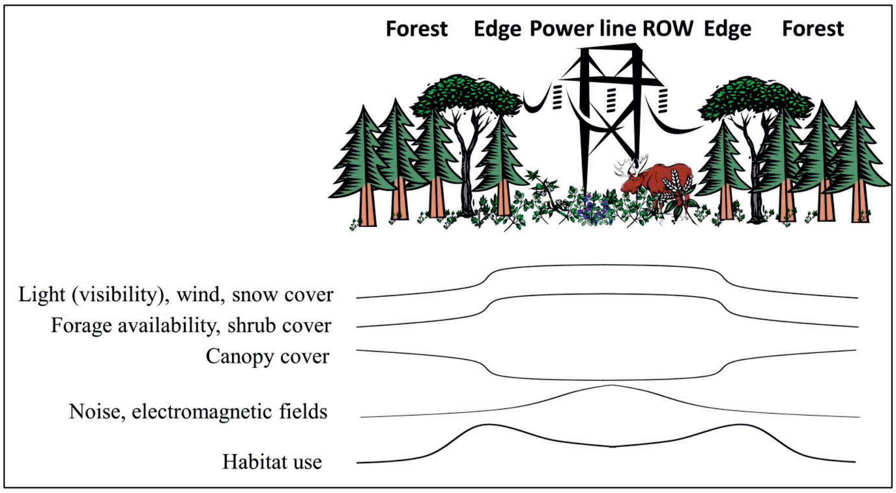

Figure 3 Possible changes in biotic and abiotic variables along power line ROWs that could affect habitat use of browsing ungulates.

However, browsing ungulates were shown to preferentially forage in power line ROWs compared to forest (Bramble and Byrnes 1972, Lamothe and Dupuy 1984, Ricard and Doucet 1999). According to the optimal foraging theory, animals should maximize the ratio of food value in relation to the time necessary for handling the food plus searching for it (summarized by Pyke et al. (1977)). Thus ungulates should preferentially forage in power line ROWs if they provide high concentrations of valuable forage.

Yet when the food intake reaches the average rate of the habitat, an animal should leave a patch according to the marginal value theorem (Charnov (1976) in Pyke et al. (1977)). Thus, ungulates should not forage in power line ROWs when their food value is below that of the surrounding forest (Joyal et al. 1984). This may be the case in the first years after clearing or as a consequence of vegetation management (Joyal et al. 1984). Protective cover may further influence the selection of foraging sites (Rieucau et al. 2007, Rieucau et al. 2009) and could be even more important for the selection of ruminating and resting sites (Takatsuki 1992). Canopy cover is lacking in power line ROWs, and shrub cover was below 20 percent in the first five years after clearing (Bramble and Byrnes 1982). This could also result in avoidance of power line ROWs (Joyal et al. 1984) or trade-off situations.

Edge effects

Forest species that avoid the openness of power line ROWs may similarly avoid the edge adjacent to them (Kroodsma 1982b, Rosselli 2002). Forest species were shown to decline in abundance (Mills 1995, Spence et al. 1996, Stevens and Husband 1998, Koivula et al. 2004, Larrivee et al. 2008) with proximity to forest edges, while species that prefer more open habitats showed the opposite trend (Johnson et al. 1979, Spence et al. 1996, Koivula et al. 2004, Pohl et al. 2007, Larrivee et al. 2008). However, this pattern is not consistent (Zabel et al. 1995, Spence et al. 1996, Menzel et al. 1999, Harding and Gomez 2006, Pohl et al. 2007). Some species appeared to avoid forest edges irrespective of the habitat, while others tracked changes of habitat related to edge distance (Kristan III et al. 2003).

The availability of shrubs was elevated in forests up to 10 m from a power line ROW compared to the interior (Luken et al. 1991, Luken et al. 1992), possibly due to an increased availability of light measured in forests below approximately 25 m from ROW edges (Pohlman et al. 2007). Lunseth (1987) observed an increasing availability of deer browse density in the proximity to a 17-year old oil or gas pipeline ROW. Studies conducted at other edges indicate highly variable effect distances, mostly ranging between 25 and 100 meters (Harper et al. 2005). Power line ROWs, similar to roads (Forman et al. 2003), have the potential to create more forest edges compared to non-linear features of equal area. However, the extent of power line ROW edge effects on vegetation and wildlife have rarely been researched (Johnson et al. 1979, Kroodsma 1982b, Kroodsma 1982a, 1984, 1987, Rich et al. 1994, Goldingay and Whelan 1997).

Forest ungulates may be able to fulfill their needs for both foraging and resting along power line ROW edges, possibly resulting in increased habitat use along those edges (**Figure 3**).

Barrier effects

Some forest species refrained from crossing power line ROWs (birds: Rosselli (2002); small mammals: Doucet and Brown (1997), Goosem and Marsh (1997), Strevens (2007), Storm and Choate (2012); ungulates: Joyal et al. (1984)), similarly as they refrained from crossing forest gaps (Desrochers and Hannon 1997) or roads traversing forests (Goosem 2001, Laurance et al. 2004, Marsh et al. 2005, Dussault et al. 2007, Rico et al. 2007, Yamada et al. 2010). However, species-specific differences existed (Goosem 2001, Bowman and Fahrig 2002, Rico et al. 2007, Yamada et al. 2010).

Few species were reported to refrain from crossing power lines in open areas (Vistnes et al. 2004, Pruett et al. 2009). However, the non-random placement of power lines or non-random movements of animals could have influenced these results (Reimers et al. 2007, Reimers and Colman 2009). If power-line ROWs pose movement barriers (**Figure 4**), they could limit access to resources (Vistnes et al. 2004). This could particularly affect ungulates that migrate long distances between seasonal ranges like moose (Bunnefeld et al. 2011) and reindeer (Tveraa et al. 2007).

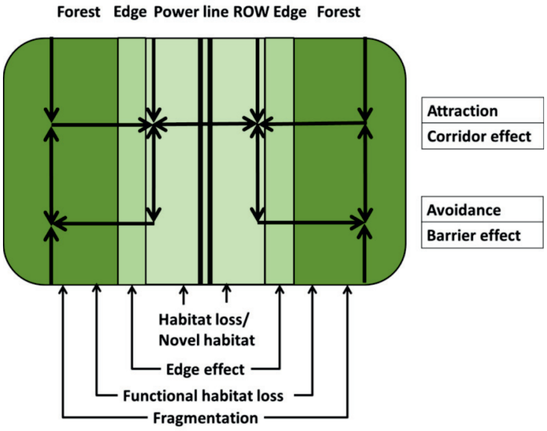

Figure 4 Potential ecological effects of power lines traversing forests. Possible implications for animal movements and habitat use are indicated by the arrows.

Population impacts

Populations that become fragmented have a higher risk of extinction (Fahrig and Merriam 1985). Smaller sub-populations are more susceptible to demographic, environmental and genetic stochasticity since stochastic events have less chance to cancel each other out (Melbourne and Hastings 2008, Wootton and Pfister 2013). Genetic isolation may further reduce productivity as a result of inbreeding depression (Griffen and Drake 2008, Haanes et al. 2013). Genetic drift was detected between populations in areas separated by roads (Keller et al. 2004, Epps et al. 2005, Lesbarreres et al. 2006, Holderegger and Di Giulio 2010, Short Bull et al. 2011, Stephens et al. 2013).

Forest edges along power line ROWs may also be a source of mortality for some prey species due to increased predator abundance (Rich et al. 1994). Increased predation rates were found along other types of forest edges, although the results are highly variable (Lahti 2001, Batary and Baldi 2004, Parker et al. 2005, Vetter et al. 2013). Some predators were reported to travel along power line ROWs (Paquet et al. 1996, Gurarie et al. 2011) and to prefer hunting in the proximity of forest edges (Laundre and Hernandez 2003, McPhee et al. 2012). Raptors perch and nest on power lines (Denoncour and Olson 1982, Steenhof et al. 1993, Prather and Messmer 2010), and humans were reported to hunt along power line ROWs (Goodwin Jr 1975). Finally, birds die in power lines through electrocution and collision (Bevanger 1995, Sergio et al. 2004, Cole and Dahl 2013).

Cumulative impacts

Although there are many aspects of power lines alone, that could affect animal behavior, habitat use and movements (**Figure 3**, **Figure 4**), they can be part of various human infrastructure developments in the same area (Nellemann et al. 2003). Roads are similar in shape but differ in their disturbance potential (Murphy and Curatolo 1987, Clair and Forrest 2009) due to traffic and the degree of habitat alteration. Female reindeer reduced area use within 1 km from ancient pitfall traps and hunting bows when accounting for the effects of power lines and roads more than roads or power lines alone (Panzacchi et al. 2013). Caribou (*Rangifer tarandus*) avoided crossing pipelines in combination with roads but did not avoid crossing single pipelines or roads.

Yet from a modeling exercise Jaeger et al. (2005) concluded that bundling roads together would have less negative effects on ungulate population persistence than distributing them evenly across the landscape. Routing power lines along exiting human features may save habitat fragments from being split into smaller pieces but could increase potential aversion and barrier effects. Recommendations for the optimal design of power line networks have yet to be made.

Power line ROW vegetation management

Power line ROW vegetation management is an important factor for the use of this habitat by wildlife (Cavanagh et al. 1976, De Waal Malefyt 1984, Confer and Pascoe 2003). Power line ROWs in Norway are cleared as needed where trees grow to a height that could interfere with the safety of the line. Although clear cuts can develop into suitable habitats for forest species, this may take a decade (Potvin et al. 2005). Vegetation management favoring an increased availability of shrubs for food and cover were shown to increase habitat use of power line ROWs by white-tailed deer (*Odocoileus virginianus*) in the USA (Bramble and Byrnes 1972, Cavanagh et al. 1976). However, the treatments involved the application of herbicides. Recommendations for improved vegetation management without the application of herbicides are also needed.

STUDY AIMS

In this thesis I aim to find out if power lines and associated forest clearings (1) affect habitat quality for moose (2) cause barrier and corridor effects (3) and cause edge effects; in order to (4) propose possible mitigation measures. In addition, I compared power line effects to those of roads and rivers and examined their cumulative effects on moose movements. My aim was to find answers to the following questions:

1. Do power lines influence moose habitat selection (**paper I and III**) and how does this compare to roads (**paper I**)?

2. Are power lines movement barriers and corridors for moose, and how does this relate to other (combinations of) linear features (**paper II**)?

3. Do power line ROW edges provide attractive feeding opportunities for moose and how far do these effects extend into forests adjacent to a power line ROW (**paper III**)?

4. How can avoidance effects of power lines by ungulates be minimized through routing and ROW vegetation management (**paper IV**)?

METHODS

Study species

Moose (*Alces alces,* **Figure 5**) are the largest living deer (Schwartz and Franzmann 2007) with a shoulder height of circa 1.8 m in central Norway (Rolandsen et al. 2010). They live in the northern hemisphere (Telfer (1984) in (Karns 2007)). Moose were selected as a model species because their movements, habitat selection and feeding behavior was expected to be influenced by the change in food and cover availability of power line ROWs (Joyal et al. 1984, Schwartz and Franzmann 2007, Bjørneraas et al. 2011, Bjørneraas et al. 2012). Moose may also react to the artificial structure of power lines, similarly to roads (Laurian et al. 2012, Beyer et al. 2013). The home ranges covered areas of circa 5-11 km^2 in central Norway (Bjørneraas et al. 2012). Some males and females were reported to migrate distances of respectively 38 and 25 km between summer and winter ranges (Rolandsen et al. 2010). Moose are therefore likely to encounter power lines alone and in combination with other linear features.

Figure 5 Moose feeding in a power line ROW in central Norway

METHODS

Although moose were relatively rare 50 years ago, they are now widely distributed in Scandinavian forests (Anderson et al. 2010). Forestry (Milner et al. 2013), low predator abundances, and female-biased sex ratio (Solberg et al. 2002) due to selective harvesting have contributed to the population increase in Norway (Anderson et al. 2010) to circa 1 moose per km^2 forest (Solberg et al. 2012). Moose are ruminants and primarily browsers. Based on Renecker and Hudson (1985), Persson et al. (2000) reckoned that moose consume respectively 30 – 40 and 10 kg of food during summer and winter.

Food limitations may have resulted in starvation (Ytrehus et al. 1999) and density dependent decrease in fecundity rates (Grøtan et al. 2009) and body mass (Herfindal et al. 2006). Moose browse mostly on birch (*Betula* spp.), although rowan (*Sorbus aucuparia)*, aspen (*Populus tremula*) and willow (*Salix* spp.) are preferred (Wam and Hjeljord 2010). Pine (*Pinus sylvestris*) is mostly consumed in winter (Wam and Hjeljord 2010). Bilberry (*Vaccinum myrtillus)*, grasses, herbs, forbs, ferns and heather are part of moose's diet in summer (Wam and Hjeljord 2010). Agricultural land is similarly selected as forests in summer and autumn (Bjørneraas et al. 2011).

The moose population in Norway is regulated through hunting (Statistics Norway 2013a). This generates economic benefits for land owners and the government (Storaas et al. 2001). Forest damage (Storaas et al. 2001, Edenius et al. 2002) and traffic accidents with moose (Seiler 2003) cause economic losses.

Study areas

The study areas were located in the boreal zone of central Norway (Karlsen et al. 2006) (64º30'N, 12º50'E, **Figure 6**, **Figure 7**). The larger study area covered Nord-Trøndelag and adjacent municipalities in Sør-Trøndelag and Nordland. The elevation ranges from sea level up to circa 1,500 m a.s.l in alpine areas towards inland. Central Norway is covered by circa 50 percent forest, of which circa 60 percent is productive (Granhus et al. 2012). The dominant tree (20-30 diameter at breast height) species are spruce (*Picea abies*) (~50%), followed by pine (*Pinus sylvestris*) (~30%) and deciduous trees (mostly birch, ~20%) (Granhus et al. 2012).

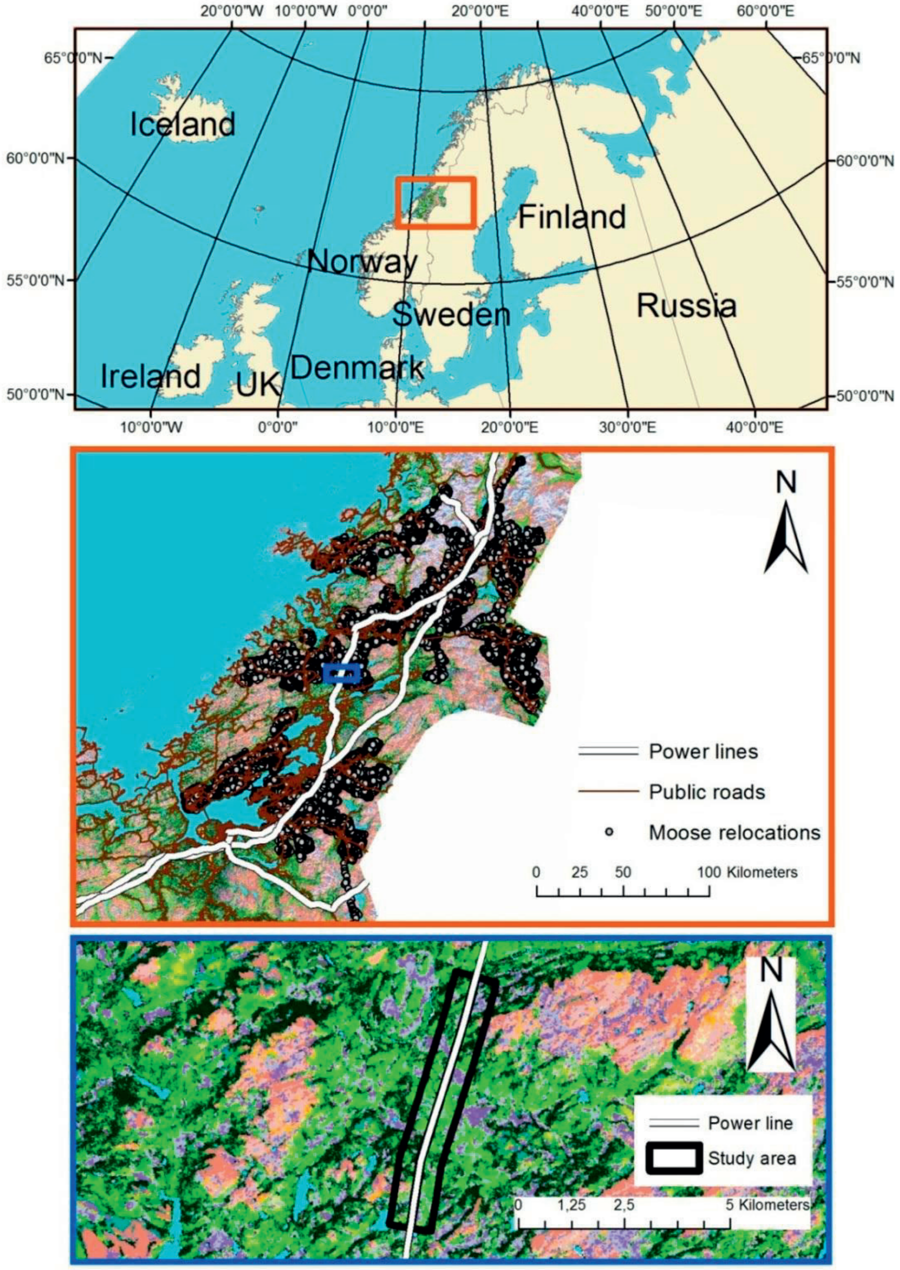

Figure 6 Map showing the large study area in Nord-Trøndelag (middle picture) and the smaller field study site in Bangdalen (lower picture) in central Norway. Central grid power lines (white thick lines), public roads (brown thin lines) and moose relocations (grey dots) during the period 2006-2010 are shown. The orange and blue rectangles correspond to the respective map sections.

Almost all of the productive forest is forestry land (Granhus et al. 2012). Clear-cutting followed by plantation is the dominant forestry regime (Skjeggedal et al. (2004) in Aasetre and Bele (2009)). Most (~90 %) of the forest is located below 500 m a.s.l. and of low to medium productivity (Granhus et al. 2012). Agricultural land, mainly distributed at lower elevations, and mire cover approximately 4 % and 11 % of Nord-Trøndelag respectively, estimated from land cover maps (Johansen et al. 2009).

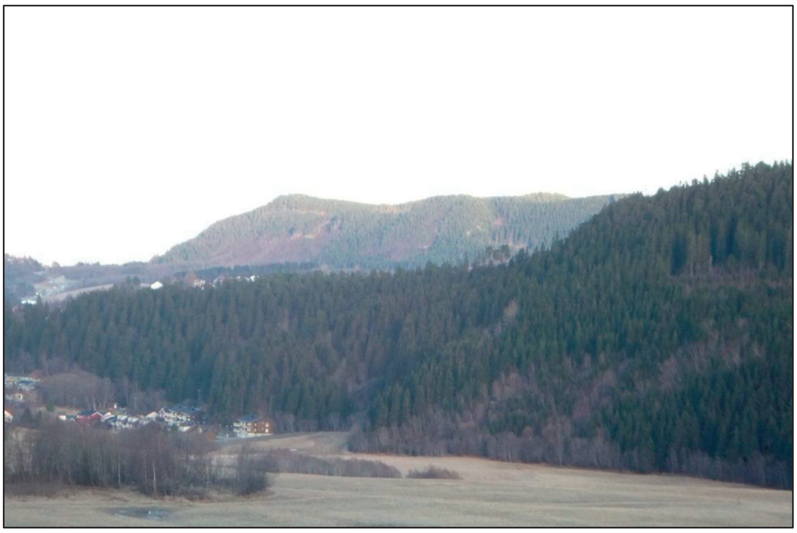

Figure 7 Landscape in central Norway (close to Trondheim, Sør-Trøndelag). Forestry and agriculture at lower elevations are the main land-use types

The mean temperature in Nord-Trøndelag is circa -2ºC in winter and 13ºC in summer (Norwegian Meteorological Insitute undated-a). Mean monthly precipitation ranges from circa 50 mm in May to 120 mm in September/October (Norwegian Meteorological Insitute undated-b). The growing season lasts from May/June until the end of September (Karlsen et al. 2006). On average, there are circa 200 (± 40 SD) days of snow with 30 (± 20 SD) cm snow cover, estimated from normalized snow cover maps.

Circa 130,000 people live in Nord-Trøndelag (Statistics Norway 2013c) corresponding to six inhabitants per km^2. The field study site in Bangdalen (64°15'16"N, 11°38'53"E, **Figure 6**, **Figure 2**) was as far away as possible from potentially confounding human influences except the almost unavoidable influences of forestry and forest roads. Less than 50 brown bears were identified in the area (Tobiassen et al. 2011). One wolf was shot in 2009 (Wabakken et al. 2011).

Data collection and analysis

GPS relocation data (paper I and II)

This study was on the scale of the selection of habitat components. The scale would correspond to third order habitat selection (Johnson 1980), if the selection was made within home ranges, but this specification was not made. 169 moose, 51 males and 118 females, were captured and equipped with GPS collars in the study area during 2006-2008. The collection of this data was part of a larger moose research project administered by Rolandsen et al. (2010). Over two million GPS relocations were initially available.

Attributes from habitat maps (Gjertsen 2007, Johansen et al. 2009), elevation maps and distances to central grid power lines, public roads, rivers and urban settlements were assigned to relocations. Movement steps were drawn by connecting straight lines between hourly start and end relocations (**Figure 8**). Forest cover, topological attributes, crossings and movements along linear features were assigned to steps from digital maps.

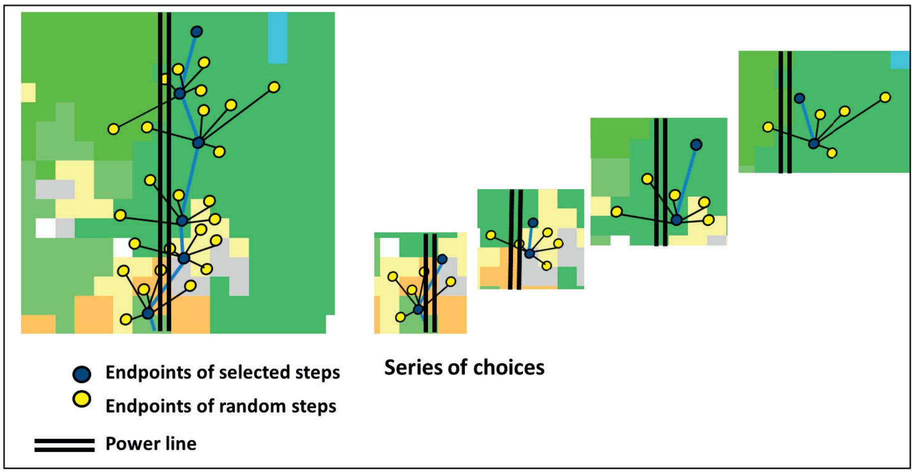

Figure 8 Illustration of the analysis method step selection function for moose GPS relocation data according to Fortin et al. (2005) and Manly et al. (2002). Moose were assumed to make series of choices along movement paths (in blue). At each choice, animals have a set of movement options available consisting of observed (endpoints in blue) and random (endpoints in yellow) steps with the same starting point. Habitat raster cells from land cover maps are depicted in the background. A hypothetical power line intersects the area.

METHODS

With the large GPS relocation dataset, the potential effects of central grid power lines on moose habitat selection and movements were researched in different habitats, seasons and terrain over a period of four years (2006-2010). A step selection function (Fortin et al. 2005) was applied. With this method, the probability of choosing observed movements steps versus random movement steps was analyzed dependent on distance to power lines and other covariates (**Figure 8**).

Road effects were included in the same analyses for the purpose of comparison and to account for the spatial dependency of power lines and roads. The effects of rivers were included for a comparison with human features in **paper II**. Furthermore, the effects of linear feature combinations were researched in **paper II**. A priory statistical candidate models including the effects of power lines, roads and environmental variables were ranked in order of their parsimony (**paper I**). In **paper II**, a priori models included barrier, corridor, a combination of both and neither of those linear feature effects on moose movements. Predictions from the top-ranking models were made for each linear feature (**paper I and II**) and for each season and gender (**paper I)**. Avoidance and attraction effects were defined by a step selection probability below and above 0.5 respectively. Two potential effects of power lines on moose movements were analyzed.

In **paper I**, avoidance of habitats in the proximity of power lines would have indicated a functional loss of habitats. Attraction towards habitats in the proximity of power lines would indicate that power lines may contribute novel habitat for moose. In **paper II**, avoidance of selecting movement steps that cross power lines would have indicated barrier effects. A preference for movement steps along power lines over movement steps in other directions indicated corridor effects. The distance to linear feature effects were modeled with non-linear terms in all analyses because a reduction in the effects can be expected with increasing distance (Laurian et al. 2012). The potentially confounding effects of habitat type, elevation, season and gender (Laurian et al. 2012, Meisingset et al. 2013) were accounted for in **paper I**. Elevation, forest cover and the topographical placement of linear features (Reimers et al. 2007) were accounted for in **paper II**.

Moose browsing and habitat use (paper III)

This study was on the scale of the selection of feeding sites, i.e. fourth order habitat selection (Johnson 1980). Random plots (n=528) up to distances of 500 meters from a 6 km long 300 kV power line stretch were surveyed for browse availability, moose browsing intensity and pellet groups at the end of spring and the beginning of summer in 2010 and 2011. Plots were circles with a radius of two meters. Birch (*Betula pubescens*), pine (*Pinus* spp.), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willow (*Salix* spp.), alder (*Alnus* spp.) and juniper (*Juniperus communis*) stems with a height between 0.6 and 4 m were counted in each plot. This height was assumed to be within the reach of moose during snowfall in winter (Danell et al. 1985).

Browsing intensity on a random trial stem was determined in each plot by the proportion of shoots that were browsed during the last and the previous years. Moose habitat use was determined by recoding pellet groups in plots. The distance to power line ROW and other types of forest edges was assigned to each plot. Forest edges were derived from intersections of the power line ROW, forest roads and rivers with forest maps (Gjertsen 2007) and from to the contours of those maps.

The data was analyzed with an information-theoretic approach (Burnham and Anderson 2002). A priori candidate models were developed including the variables distance to forest edge, edge type, stem availability, elevation and stem height where appropriate. Predictions from models up to two AIC points from the top-ranging model were averaged by their model weights.

Literature review (paper IV)

To get a better understanding on the potential effects of power lines on ungulates, the existing peer-reviewed literature was reviewed. Because of the limited literature on power line effects, reviews on road effects (Forman and Alexander (1998), Spellerberg (1998), Seiler (2001), , Coffin (2007), Fahrig and Rytwinski (2009), Benitez-Lopez et al. (2010)) and relevant references therein were also consulted. The results from the studies were synthesized into a concept of which factors possibly influence avoidance and attraction effects of power lines on ungulates. Based on the concept, recommendations for the routing of power lines and for the vegetation management of the rights-of-way were made.

MAIN RESULTS AND DISCUSSION

Do power lines influence moose habitat selection (**paper I and III**) *and how does this compare to roads* (**paper I**)?

The effects of power lines and roads varied with habitat, season and gender. Power lines were not included in the top models for the season spring and summer, avoided only in certain habitats in autumn and appeared to be a source of attraction in winter. Novel feeding habitats in and along power line ROWs in times of energetic deficit may have been the cause this attraction. Human hunting near power lines (Goodwin Jr 1975) could have caused the avoidance of some habitats surrounding power lines in autumn. Avoidance did not increase in open habitats. The results indicate that power lines did not result in a functional loss of habitats.

Power lines had weaker effects on moose habitat selection than roads. Females avoided roads more than males in spring and summer, but were able to tolerate roads in old and deciduous forests in autumn. Feeding opportunities in agricultural land close to roads in summer and autumn and sufficient cover in old spruce and deciduous forests may have counteracted possible road disturbances. Roads were not included in the top model for winter, possibly because moose could not afford to lose feeding opportunities along road edges (Rea 2003) in this season. Although elevation was included as a covariate in all models, the use of lower elevations during winter (Rolandsen et al. 2010) could have also had an effect. Roads and power lines were generally situated at lower elevations in the study area. The lack of power line avoidance contrasts reductions in reindeer abundances in the proximity of power lines (Nellemann et al. 2001, Vistnes and Nellemann 2001), indicating that reindeer avoided areas close to power lines.

Power lines were expected to have a lower disturbance potential than roads, because they emit less noise and they are non-moving objects in contrast to road traffic. Noise levels at central grid power lines were between 40 and 50 dB in light rain (Flydal et al. 2010), while road surfaces with traffic speeds between 50 and 100 km per hour emitted noise between 93 and 100 dB (Aksnes and Evensen 2009).

Moose traversing forests may not become aware of the presence of a power line until they can see or hear it in the proximity of the open corridor. Experiments with reindeer indicated that this species can hear power lines only up to a distance of 79 m (Flydal et al. 2010). Human activity may have also been higher in areas surrounding roads (Lykkja 2009) compared to central grid power lines. The results from this analysis point towards potential benefits of feeding opportunities in power line ROWs for moose in winter.

Are power lines movement barriers and corridors for moose, and how does this relate to other (combinations of) linear features (**paper II**)?

No avoidance of crossing power lines was found, unless the topographical placement of power lines along contour lines impeded movements across them. Neither did moose avoid crossing roads or rivers that traversed open habitats and were not aligned along contour lines. However, moose avoided crossing roads and rivers in forests, indicating that the forest gap created by linear corridors impeded movements. Feeding opportunities in power line ROWs may have encouraged moose to traverse such gaps.

Moose increased movements along power lines when getting closer to power lines but did not prefer moving along power lines over crossing or moving away from power lines when being in close enough proximity (25 m distance) to cross them. Moose preferred moving along roads and rivers (although not significantly for rivers) over crossing them when traversing forests. Power lines had the least corridor and barrier effect as expected, while roads had the strongest effects when moose were travelling through forest. Road/river combinations increased barrier and corridor effects as predicted, but the effects of power line/river combinations were not consistent. A larger sample size with regards to linear feature combinations would have been necessary to make more reliable predictions. The results suggested that combinations of linear features may increase barrier effects compared to single linear features.

The results indicate that power lines do not pose barriers for moose movements and cause less of a corridor effect compared to roads and rivers when moose are in close proximity. In contrast, reindeer in Norway were suspected to avoid crossing power lines in open habitats, resulting in a reduction of feeding activity in areas separated by power lines (Vistnes et al. 2004).

The lack of vegetation and an increased width of the corridor were also shown to impede forest ungulate crossings of power line ROWs locally (Doucet et al. 1983, Joyal et al. 1984). These effects were not taken into account. Also, moose responded more strongly with the change of their movements when getting closer to power lines and roads than rivers, indicating that disturbance may have had an influence. However, the results from **paper I** indicate that moose can tolerate possible disturbances.

Do power line ROW edges provide attractive feeding opportunities for moose and how far do effects extent into forests adjacent to the power line ROW (**paper III**)?

The availability of stems in the power line ROW was above that of other open areas but below that of forest in the study area. A short time period since clearing site may have been the reason for this (Bramble and Byrnes 1982). It appeared that habitat type rather than distance to power line ROW edge influenced the availability of stems for browsing. The abundance of the main browsing species birch did not peak at the edge as expected but at 100 meters distance from forest edges.

Probably the interspersion of open areas and forestry in the study area created a mixture in successional stages. However, the less abundant pine was mostly found within 100 meters from forest edges. Pine can be an important component of moose's winter diet (Wam and Hjeljord 2010). Also, shoots on birch stems increased from forest interior towards open areas, possibly facilitated by an increasing availability of light.

Moose browsed a slightly higher proportion of shoots during the year preceding the study in open areas near power line ROW edges compared to other types of forest edges. Browsing during the previous year's appeared to be influenced by the availability of stems in the study area.

Habitat use indicated by pellet groups was indifferent of the type of edge (i.e. power line ROW or other forest edge) and peaked at approximately 50 m distance from the edge. The better canopy cover protecting from snow and potential predators could have been the reason for this (Thompson and Vukelich 1981, Rieucau et al. 2007). The results indicate that moose were tolerating possible disturbance from power lines. Moose were mostly using forests within 50 – 100 m from power line ROW and other types of forest edges, apparently influenced by the availability of food and cover.

MAIN RESULTS AND DISCUSSION

How can avoidance effects of power lines by ungulates be minimized through routing and ROW vegetation management (**paper IV**)*?*

From the reviewed literature two major sources of avoidance were identified, which are species-specific. Reindeer inhabiting open habitats are supposed to associate power lines with danger (Vistnes et al. 2004), avoid areas in the proximity of power lines (Nellemann et al. 2001, Vistnes and Nellemann 2001, Vistnes et al. 2001) and crossing power lines (Vistnes et al. 2004). The opposing argument is that reindeer, similar to other ungulates, are able to adapt to disturbances (Bergerud et al. 1984, Reimers et al. 2007, Reimers and Colman 2009) and should not waste time and energy on non-lethal disturbances. The influence of confounding factors like food availability, elevation, topology, and other human features in the proximity of power lines in the analysis of non-experimental studies and possible reasons for species-specific effects were discussed.

For forest ungulates, the lack of food and cover in power line ROWs appeared to be the major determinant of the avoidance of cleared areas under power lines. Forest ungulates were shown to preferentially forage in power line ROWs providing sufficient food and cover, and no signs of behavioral disturbance by the structure were found. However, rigorous studies on wild ungulate behavior under power lines are rare (Flydal et al. 2009). In general, ungulates appeared to be most disturbed by human activity in times of calving.

Possible mitigation measures include (1) avoid routing power lines through ungulate habitat, (2) avoid constructing power lines in areas and times of calving, (3) route power lines through food-poor old coniferous forests instead of food-rich young or deciduous forests, (4) increase food and cover availability in power line ROWs through vegetation management and (5) minimize noise and electromagnetic fields from power lines and human disturbance along power lines.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The results from **paper III** and Joyal et al. (1984) indicated that moose reduced habitat use in power line ROWs compared to surrounding forest providing better cover. Although the availability of browse in the power line ROW was below that of adjacent forest in the field study area, moose appeared to be attracted towards power line ROWs in winter across the larger study area (**paper I**) (**Figure 6**).

This apparent contradiction may have been influenced by site-specific variations food and cover availability dependent on the time since clearing (Bramble and Byrnes 1972, De Waal Malefyt 1984, Ricard and Doucet 1999). While the power line ROW in field site appeared to be recently cleared, vegetation regrowth in other areas may have provided more abundant browse. A preference towards lower elevations closer to power lines by moose in winter (Rolandsen et al. 2010) could have also influenced attraction effects. As pointed out in **paper IV**, confounding factors may influence the analysis of non-experimental data.

Disturbance by the physical structure appeared to be of minor importance (**paper I and III**) or was compensated for by the availability of browse in power line ROWs. In contrast to roads, power lines did not appear to cause a functional loss of moose habitat (**paper I**). The avoidance of power lines in certain habitats in autumn may have been caused by human hunting in the proximity of power lines.

The avoidance of crossing roads and rivers in forests, but not in open habitats, indicated that moose avoided crossing linear forest gaps (**paper II**). The availability of shrubs in power line ROWs may have encouraged moose to cross power line ROW clearings, resulting in no apparent barrier effects. However, a disturbance potential could not be fully excluded (**paper II**). Possibly moose could not afford to lose feeding opportunities in power line ROWs, especially in times of energetic deficit during winter (**paper I**). To reduce potential aversion effects, alternative management regimes to full clearing that increase the availability of food and cover inside power line ROWs are recommended (**paper IV**).

Several studies seem to suggest that maintaining intermediate levels of succession in power line ROWs has co-benefits for other mammals and birds (Cavanagh et al. 1976, De Waal Malefyt 1984, Confer and Pascoe 2003, Strevens 2007).

However, the effects can be species-specific (Yahner et al. 2001a, Lanham and Simmons 2002). Some butterflies (Lensu et al. 2011, Berg et al. 2013, Komonen et al. 2013), scrubland birds (Confer 2002, Confer et al. 2008), bees (Russell et al. 2005) and snakes (Yahner et al. 2001a) prefer earlier to later successional stages.

Management adapted to the local conditions and shifting ROW treatments may be necessary depending on the conservation goals for the species in question and surrounding landscape (Arner 1997). In Europe, an increase of forest ungulate populations is undesirable from a conservation perspective (Fuller and Gill 2001, Edenius et al. 2002, Côté et al. 2004, Gordon et al. 2004). However, power line ROWs may potentially reduce forest damage by providing alternative feeding areas.

FUTURE PROSPECTS

Paper II indicated that combinations of linear features may increase barrier and corridor effects compared to single linear features. It would be important to find out if barrier and aversion effects are greater for combinations of parallel power lines than single power lines (Joyal et al. 1984). The willingness to cross power line ROWs may further depend on food and cover availability inside ROWs. These parameters should be included in further analyses to make recommendations for power line routing and management.

The applicability of the suggested alternative vegetation management regimes in **paper IV** needs to be tested in field studies, ideally over several years and with sufficient number of replicates and controls. Possibly the detection edge effects in **paper III** was hampered by the variation of the forest structure in the study area. Repeating the study in an area with more homogeneous forest cover and increasing the surveyed area and number of field seasons would help to derive more firm conclusions.

Although results from these studies (**paper I and III**) and field observations by Goodwin Jr (1975) suggest that forest ungulate behavior is not disturbed by power lines, experimental studies similarly to Flydal et al. (2009) are lacking. Surveying fecal glucocorticoid concentrations and other disturbance indicators (Tarlow and Blumstein 2007) would help to find out if power lines are anthropogenic stressors (**paper IV**). To remove the potentially confounding effects on animal habitat use and behavior, before-after-control-impact (BAIC) studies would be ideal (**paper IV**).

FUTURE PROSPECTS

This and most other (Goodwin Jr 1975, Joyal et al. 1984, Lamothe and Dupuy 1984, Nellemann et al. 2001) research concentrated on the effects of central grid power lines on ungulates. However, these large power lines with wide corridors may only constitute a small proportion of the total grid (Statistics Norway 2011). It is uncertain to what extent lower voltage power lines effect ungulates (Vistnes and Nellemann 2001, Reimers et al. 2007). The corridor is narrower and the construction of the power line is smaller but there could be cumulative effects. Population impacts of routing power line ROWs through wild ungulate habitats have, from the reviewed literature, not been researched.

Compared to moose, fragmentation effects of power line ROWs could be more severe for smaller-bodied forest species like small mammals (Strevens 2007, Storm and Choate 2012) or insects. Road clearings of 20 m width completely inhibited crossings of some small mammal species (Goosem 2001). Abundance and richness of macroinvertebrates decreased in the proximity of roads traversing forest (Haskell 2000). Frogs refrained from venturing into clear-cuts (Chan-McLeod 2003). Relative abundances of forest birds declined with proximity to an open power line ROW (Rosselli 2002).

Knowledge about the use of power line ROWs and associated edges for natural predators is scarce (Paquet et al. 1996, Gurarie et al. 2011). Migratory birds (Wiltschko 1968, Mouritsen and Ritz 2005, Wiltschko et al. 2010), bats (Holland et al. 2006), some rodents (Kimchi and Terkel 2001, Deutschlander et al. 2003, Oliveriusova et al. 2012), elasmobranchii (sharks, skates and rays) (Kalmijn 1982), turtles (Putman et al. 2011), some fish (Taylor 1986, Souza et al. 1988) and cetaceans (Klinowska 1985, 1986) are suspected to use the earth’s magnetic field for orientation. Whether electromagnetic fields of power lines influence the orientation of those species is not known or uncertain (Gill and Taylor 2001, Ohman et al. 2007). These species could be candidates for further research.

In general, ecological research, especially such with management implications, would benefit from interfering with systems rather than observing them to make more reliable predictions. A more precise and uniform definition of ecological terms, e.g. shrub, tree, forest (Harris and Silva-Lopez 1992), edge (Murcia 1995), preference and avoidance would aid in the repeatability of the studies. Such an attempt was made in **paper I and II**. This might stimulate similar efforts.

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Paper I

COMPARATIVE EFFECTS OF POWER LINES AND ROADS ON MOOSE (*ALCES ALCES*) HABITAT SELECTION

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Abstract: The planned extension of the high-voltage overhead power line grid in Norway is expected to increase loss and fragmentation of wildlife habitat. The public road network is also expanding. However, power line rights-of-way (cleared areas under power lines) and roadside edge vegetation can provide attractive feeding opportunities for moose (*Alces alces*). While some land owners wish to maintain high moose densities for selling hunting licenses, others are concerned about damage to forest vegetation or the risk of moose-vehicle collisions. The disturbance or attraction potential of power line ROW and roads to moose is therefore of substantial interest. We applied a step selection function on GPS relocation data of 58 moose individuals expecting that central-grid power lines are avoided less than public roads based on their differential disturbance potential. We expected greater avoidance in open habitats because these do not shield from disturbance, less avoidance in winter when moose are in a state of energetic deficit and greater avoidance by female moose. We found no evidence for power line ROW avoidance but moose avoided areas close roads. However, seasonal and gender-specific differences existed. We did not detect greater avoidance in open habitats. These results will help to develop guidelines for the routing of power lines and roads through different habitat types to minimize disturbance to moose while balancing the interests of land owners and conservationists.

Keywords: power lines, roads, moose, *Alces alces,* Norway, step selection function, habitat, season.

INTRODUCTION

Several studies have found that moose and other ungulates avoid areas near roads (Dyer et al. 2001, Fortin et al. 2005, Coulon et al. 2008, Laurian et al. 2012) and avoid crossing roads (Dyer et al. 2002, Dussault et al. 2007, Laurian et al. 2008, Beyer et al. 2013). Previous research also suggests that reindeer (*Rangifer tarandus tarandus*) in Norway (Nellemann et al. 2001, Vistnes and Nellemann 2001, Nellemann et al. 2003) avoid using areas near power lines and that power lines pose barriers to reindeer migration (Vistnes et al. 2004). The reason for such avoidance or barrier effects may be the physical structure and noise emitted by power lines (Flydal et al. 2009, Flydal et al. 2010) and roads (Gagnon et al. 2007a, Gagnon et al. 2007b). In addition, ungulates like moose that avoid open habitats (Bjørneraas et al. 2011) may also avoid the openness of power line or road corridors traversing otherwise continuous forests. Power line rights-of-way (ROW) and roads may thus be disturbing. However, young vegetation in power line ROW (Takatsuki 1992, Ricard and Doucet 1999, Doucet and Thompson 2002, 2008) and roadside edge vegetation (Rea 2003) can provide feeding opportunities and could result in trade-off situations or even attraction effects. Joyal et al. (1984) found that moose frequented power line ROW less often than control forest while Ricard and Doucet (1999) found that moose use power line ROW for feeding more than surrounding forest in winter.

Our research was motivated by concerns about wildlife impacts that could arise from the planned expansion of the Norwegian power line grid (Statnett SF 2011, Norwegian Ministry of Petroleum and Energy 2012) and the similarity of power lines with roads because of their linear shape. The Norwegian central power line grid operator Statnett is planning to build more than 200 km of new power lines per year until 2020 (Statnett SF 2011) to satisfy the increased requirements for the transmission of electricity (Ministry of Petroleum and Energy 2006, Mostue and Moengen 2011). High-voltage power lines raise most of the political and public debate because of their visual and potential environmental impacts (Norwegian Ministry of Petroleum and Energy 2012). However, power lines below 220 kV make up 76% of the ~ 193,000 km overhead power line grid in Norway (Statistics Norway 2011a). Furthermore, ~ 93,000 km public and ~ 126,000 km private, forest and tractor roads exist (Norwegian Mapping Authority 2012). The road network is still expanding; between the years 2000 and 2010, 2,467 km of public roads and 1,162 km of forest roads were built (Statistics Norway 2004, Brunvoll and Monsrud 2011, Statistics Norway 2012).

We chose moose (*Alces alces*) as a model species to better understand the avoidance and attraction potential of power lines and roads, because moose select habitats, mainly forest, according to their value for food and cover (Bjørneraas et al. 2011, 2012). When power lines or roads intersect forests, the close proximity of young feeding plants in combination with nearby forest cover could make such edge areas attractive for ungulates (Waring et al. 1991, Rea 2003, Seiler 2005, Wirth et al. 2008). Moreover, moose is an ecologically and economically important species in Norway. Intense browsing by moose is expected to reduce forest regrowth (Edenius et al. 2002), which results in financial losses for land owners (Storaas et al. 2001). Other land owners are interested in maintaining high moose densities for selling hunting licenses. Importantly, 1,462 moose-vehicle collisions occurred in Norway during the hunting year 2011/2012 (Statistics Norway 2011b). Economic losses through collisions were estimated to amount to 11-17 million € (equivalent to ~ 8-12 million USD) (Seiler 2003). Potential avoidance or attraction effects of power lines and roads in different habitats that could lead to a reduction or concentration of moose are therefore of substantial interest.

Responses to power lines or roads may easily be confounded with responses to habitats or landscape structures which power lines or roads intersect or parallel (Rowland et al. 2000, Gagnon et al. 2007a, Reimers et al. 2007, Frair et al. 2008, Roever et al. 2010, Grosman et al. 2011, Meisingset et al. 2013). Reimers et al. (2007) could not detect avoidance of a 66 kV power line by Norwegian reindeer when accounting for elevation. Environmental variation, movement corridors or hunting pressure could have been alternative explanations of avoidance reported in earlier studies (Reimers 2001). Yost and Wright (2001) observed increased sightings of moose away from a road in Alaska but acknowledged that this pattern could have been caused by the increased availability of forage at larger distances. Ball and Dahlgren (2002) found increased browsing intensity by moose near a highway in Sweden and suggested that moose may have avoided crossing this highway. However, an increased availability of browsing plants near this highway could have been an alternative explanation.

In addition, males and females may respond differently (Laurian et al. 2012). Bjørneraas et al. (2011, 2012) found that female moose with young avoid open food-rich habitats more than males; and prefer habitats with greater cover. Lykkja (2009) showed that males used areas near houses more than females when human activity was low. Differential responses may also be expected towards disturbance and feeding opportunities of power line ROW and road edges. Based on the greater disturbance potential of roads versus power lines and the differential selection of habitats by gender we expected that: (1) roads are avoided more than power lines, (2) avoidance increases in open habitats because those do not provide protective cover, (3) avoidance decreases during winter and at the onset of the growing season when moose are in a state of energetic deficit and additional browsing resources are most important, and (4) female moose avoid power lines and roads more than male moose. The aim of the study was to validate these four predictions.

METHODS

Study area

The study area (23,081 km^2) was situated in central Norway mostly in the county of Nord-Trøndelag (Fig. 1). The area is dominated by spruce (*Picea abies*) forest and agriculture at lower elevations. The average elevation was 454 (± 244 SD) meters a.s.l., and ranged from sea level up to 1,694 meters a.s.l.. The Norwegian central grid operator Statnett provided us with the power line routing data. The voltage of those power lines was not made available, but judging from their corridor widths between 32 and 38 meters, those would typically carry voltages between 220 and 420 kV (Bevanger and Thingstad 1988). These power lines amounted to 763 km in the study area. We were not able to obtain accurate routing data for power lines of lower voltages. Public roads were extracted from a road database from the Norwegian Mapping Authority (Norwegian Mapping Authority 2012). Those encompassed highways, national roads, county roads and municipal roads. The total length was 3,739 km outside urban settlements. Roads were on average 135 (± 134 SD) meters a.s.l. and central-grid power lines 287 (± 143 SD) meters a.s.l.. We did not consider lower voltage power lines, private, tractor and forest roads, because they are present throughout moose home ranges and were thought to have limited impacts.

Moose data

Data preparation

GPS relocation data of 169 animals was available for analysis, irrespective of their home range location with respect to roads or power lines. Those were captured between February 2006 and March 2008. Erroneous locations were removed using the method described by Bjørneraas et al. (2010). We removed relocations less than five kilometers away from the Swedish border, because moose movement could have been influenced by features across the border unknown to us. We did not consider relocations on islands in the municipality Vikna, where moose movements were restricted. For each observed movement step, a straight line between hourly start and end relocations, we created five random steps taken from the distribution of relative turning angles and step lengths (Fortin et al. 2005). Only individuals with at least 1,000 steps were used for this. Similar to Latham et al. (2011) we did not consider steps of less than ten meters length as movements and eliminated those.

We accounted for directionality as in a correlated random walk model (Kareiva and Shigesada 1983). We assigned distance values for power lines, roads and urban settlements to endpoints of steps using a 10 x10 m distance raster created with ArcView version 10 (ESRI 2011). Forest types were retrieved from a polygon forest map (Gjertsen 2007, Norwegian Forest and Landscape Institute undated). Positions outside forest polygons received the attributes open land, mire or agriculture from a raster map with a resolution of 30 x 30 meters (Johansen et al. 2009). A description of the habitat types is provided by Bjørneraas et al. (2011). We defined spruce forests above 40 years of age as old spruce forest.

Further data selection

We included only individuals that were found at least once within a two kilometer buffer from power lines for further analysis. Those consisted of 17 males and 41 females with 9,268 (± 6,218 SD) steps per individual. We found moderate correlations between distances to public roads and urban settlements ($r = 0.32$). To avoid potentially confounding effects of other human activity we removed all relocations within 2.5 kilometers from urban settlements. The frequency of relocations dropped progressively above distances of 300 meters from roads and power lines. The decline was less sharp for power lines. We therefore assumed that moose did not respond to roads or power lines above distances of two kilometers. We fixed the distance effect above this cut-off value to zero by setting distances above two kilometers to two kilometers. Finally we split the dataset into seasons, following Bjørneraas et al. (2011), and gender.

Statistical analysis

Model selection

We used conditional logistic regression to model the probability of selecting observed movement steps versus random movement steps (Manly et al. 2002) in response to habitat, elevation and distance to power lines and roads. Non-linear effects of elevation, power lines and roads were modeled with restricted cubic splines (Harrell 2001b) with three knots or four knots when convergence could not be achieved otherwise. We checked for partial autocorrelation of deviance model residuals and calculated robust standard errors through clustering (Fortin et al. 2005) assuming independence between individuals. Based on our hypotheses, we derived seven candidate models and ranked those after their QIC (quasi-likelihood under independence criterion) values (Pan 2001, Craiu et al. 2008, Barnett et al.

2010). QIC was used instead of AIC (Akaike 1974) because steps within clusters were not independent. As with AIC values, QIC values decrease with parsimony (Craiu et al. 2008). Because QIC differences were two for top models in spring we also report model weights (Burnham and Anderson 2002). The basic model included only habitat and elevation (m1 in Table 1). Since we expected greater effects of roads (m2) than power lines (m3), we added effects of each, and in interaction with habitat (m4 and m5). Finally we wanted to find out if effects of power lines (m6 and m7) could further improve models already containing road effects. We subsequently ran the top models on males and females.

Significance tests

The significance of variables in the top models was tested from the Wald statistic, which is Chi-square distributed with the degrees of freedom equal to number of parameters. Since all variables were significant ($P < 0.05$), we calculated a penalized Wald statistic (Fig. 2) by subtracting twice the degrees of freedom (Harrell 2001a). These values increase with significance and are penalized by the number of parameters. We calculated the penalized Wald statistics for the combined effects of each variable including its interactions where applicable (Harrell (2012); Fig. 2). All statistical analyses were done in R version 14.2 (R Development Core Team 2012). We used a Cox proportional hazard model (cph) for conditional logistic regressions and restricted cubic splines from the R-package rms (Harrell 2012).

Model predictions

We predicted step selection probabilities for the most parsimonious models as follows (Manly et al. 2002):

$$P_i = \frac{\exp(\beta_1 * x_{i1} + \beta_2 * x_{i2} + \cdots + \beta_p * x_{ij})}{\exp\left(\beta_1 * x_{i1} + \beta_2 * x_{i2} + \cdots + \beta_p * x_{ij}\right) + \exp\left(\beta_1 * x_{ba1} + \beta_2 * x_{ba2} + \cdots + \beta_p * x_{baj}\right)}$$

where P_i is the probability of selecting the *i'th* unit or step over the alternative unit or step *ba* and β_j are the estimated coefficients for the environmental variables x_{ij}. *ba* in the second denominator is synonymous for baseline. Previously, relative step selection probabilities were derived from a resource selection function following the exponential form equivalent to the numerator in the above equation (Fortin et al. 2005, Coulon et al. 2008, Latham et al. 2011). Our interpretation of the step selection probability is the probability of moving from the baseline distance and habitat (2 kilometers to the nearest power line or road in old spruce forest) to a given distance and habitat. We use the terms avoidance/attraction if the probability of movement towards power lines or roads from the baseline distance and habitat is below/above 0.5. We describe preferences for different habitat types dependent on the direction of the predictions but irrespective of the definition of attraction or avoidance.

Model validation

To check how well the most parsimonious models predict we used five-fold cross validation (Boyce et al. 2002). We scaled linear predictions from the seasonal model and data to lie between zero and one applying equation 2 in Johnson et al. (2004). From these predictions we derived ten bins of approximately equal size. From each seasonal dataset we randomly sampled five test and training datasets. We predicted from models built with the training and the full datasets for the test datasets. Low RMSD and high correlations between the frequency of the scaled linear predictions from models built with the training and full data in bins indicate that the model predicts well.

RESULTS

Model selection, importance of variables and predictive ability

Models containing power line-habitat interactions (m5, Table 1) were less parsimonious than models containing road-habitat interactions (m3), except for winter. The most parsimonious model for winter (m4) contained only power line, but no road effects. The most parsimonious models for spring (m3) and summer (m2) contained only road, but no power line effects. The top model for autumn (m7) contained both road and power line effects. The evidence for the most parsimonious models being the best of candidate models was strong except for spring, where the model weight was 0.68 (Table 1). A model including power line effects followed with a weight of 0.32. Habitat including its first order interactions was the most important variable for all seasons (Fig. 2) and both genders (Appendix, Fig. 1). Distance to power lines and roads were more important than elevation in autumn (Fig. 2). Otherwise elevation followed habitat as the second most important variable (Fig. 2). The importance of roads increased in relation to habitat in summer and autumn (Fig. 2) Habitat was more important for females than males (Appendix, Fig. 1) in relation to other variables. The top models predicted well according to RMSD (< 0.02) and Spearman's rank correlations ($r > 0.6$, $P < 0.05$).

Seasonal and gender-specific responses

Step selection varied among seasons and between genders (Fig. 3 A - P). Distance to power lines was not included in the top models for spring and summer (Fig. 3 A, C, E, G). Males avoided areas less than 1 km from roads in pine forests in spring but did not respond strongly to roads otherwise (Fig. 3 B). Females avoided roads in all habitats and avoided young spruce forests more than old spruce forests in the proximity of roads (Fig. 3 D). In summer, males were attracted towards open, land, mire and agriculture less than 250 m from roads and towards forests less than 0.5 – 1 km distance from roads (Fig. 3 F). In contrast, females avoided areas less than 0.5 km from roads in all habitats (Fig. 3 H). Open, land, mire and agriculture were least avoided in summer (Fig. 3 E - H). In autumn, there was no clear trend in step selection towards power lines. Both genders avoided power lines in pine forests and were slightly attracted towards power lines in young spruce forests (Fig. 3 I, K). Females avoided power lines in open habitats more than males (Fig. 3 I, K). Males were mostly tolerating roads in autumn but were less attracted towards young spruce forests and pine forests less than 1 km from roads (Fig. 3 J). Females avoided roads in young spruce forests, pine forests and open habitats less than 0.5 km distance (Fig. 3 L). In winter, moose were attracted towards power lines in all forest types (Fig. 3 M, O). Open habitats were strongly avoided in this season (Fig. 3 M - P). Roads were not part of the winter model (Fig. 3 N, P).

DISCUSSION

The objective of this study was to compare moose gender-specific responses to power lines and roads while accounting for the seasonal selection of nearby habitats. The lower parsimony of models containing power line effects compared to models that contained road effects indicates that moose step selection was less determined by power lines than by roads. This may arise because of differential disturbance levels of power lines versus roads due to noise and visual stimuli. Noise levels at high-voltage power lines may range between 40 and 50 dB in light rain (Flydal et al. 2010). An audiogram for reindeer suggests that this ungulate species can hear power line noise only up to a distance of 79 m (Flydal et al. 2010). In contrast, the reference value for noise levels of road surfaces in Norway lies between 93 and 100 dB

(Aksnes and Evensen 2009). This represents traffic speeds between 50 and 100 km per hour. Gagnon et al. (2007a) showed that red deer (*Cervus elaphus*) road crossings declined with increasing traffic volume which supports increased disturbance potential due to traffic. Moreover, while road surfaces do not constitute habitat, power line ROW traversing forests may be considered as such. The avoidance of roads by females during spring and summer supports our prediction that moose avoid roads more than power lines. However, males appeared to be more tolerant. Moreover, we found attraction effects of power lines in winter. Similarly, Neumann et al. (2013) found that moose moved faster less than 125 m from roads indicating disturbance while power lines had no effect.

Contrary to prediction two we found no evidence for increased avoidance in open habitats, except for road avoidance by males in spring and power line avoidance by females in autumn. The lack of clear responses towards power lines in autumn may have been caused by irregular movements because of human hunting (Ericsson and Wallin 1996, Neumann 2009) and rutting activity (Phillips et al. 1973, Cederlund and Sand 1994, Neumann et al. 2009). Hunting in the proximity of power lines and roads could have led to an increased importance of power lines and roads in this season. The apparent attraction effect of roads in summer and autumn may be explained by the seasonal selection of agricultural land (Bjørneraas et al. 2011) and the higher productivity of forests in the proximity of roads (Bjørneraas et al. 2012). Meisingset et al. (2013) found that red deer in Sweden became more likely to use areas close to roads during darkness in summer and autumn and less reluctant to cross roads close to pastures. The better canopy cover in old, mixed and deciduous forest compared to pine and young spruce forest (Korhonen et al. 2006) and the high availability of food in mixed and deciduous forest (Bjørneraas et al. 2011) may have also counteracted disturbance by roads in spring and autumn. Females avoided young spruce and pine forest more than males in the proximity of roads possibly because they lacked cover to shield from disturbance.

The model predictions in winter support our expectation that avoidance decreases in winter, when moose are in a state of energetic deficit. The attraction towards power line ROW may be explained by their provisioning of browsing resources. Ricard and Doucet (1999) compared availability and use of browsing twigs by moose in power line ROW and control areas in forest in winter. Moose browsed approximately seven times more of the available twigs in power line ROW than in adjacent forest despite the overall lower availability of twigs. Irregular clearing regimes, as applied in Norway, may result in local concentration of browsing plants in power line ROW dependent on the time since clearing (Ricard and Doucet

1999). The intensity of browsing an area may increase with the availability of browsing plants in that area as moose have to spend less time searching for food (Eplett 2012). This could result in a greater overall use of power line ROW for browsing in winter. Similar to power line ROW, roadside edges can offer attractive browsing opportunities (Rea 2003). Moose may trade the availability of forage with the avoidance of roads resulting in no obvious responses in winter.

However, moose's seasonal preferences for elevation could have also had an influence. Power lines and particularly roads were generally situated at lower elevations within the study area. Moose tend to migrate towards lower elevation winter ranges in autumn and higher elevation summer ranges in spring (Ballard et al. 1991); a pattern also known from other ungulates (Mysterud 1999, Luccarini et al. 2006). Gundersen et al. (2004) found that moose in Norway increased the use of winter feeding stations when those were closer to the bottom of side valleys. Neumann et al. (2012) showed that moose-vehicle collisions in Sweden were more likely in autumn and winter. This is in accordance with our findings of increased movement probabilities towards roads in autumn, and avoidance of roads by females in spring and summer. However, opposite trends to this general pattern have been reported (Hauge and Keith (1981), Andersen (1991), Schwartz and Franzmann (2007)), the timing of this migration can vary considerably (Bunnefeld et al. 2011) and not all individuals migrate (Cederlund and Sand 1992).

Females were more attracted towards power line ROW in winter than males but appeared to be more disturbed by roads than males in the other seasons. Possibly males were better in tolerating disturbance from roads while exploiting higher productivity forests (Bjørneraas et al. 2012) and agricultural land, that are typically found closer to roads. In contrast, roads may reduce the willingness of female moose to access higher quality feeding habitats in times of raising young in spring and summer. Females were also less likely to move towards power lines in autumn and may in general be less willing to use lower elevations closer to human disturbance. Prediction four stating greater avoidance by females was thus supported. In contrast, Laurian et al. (2012) found that males avoided roads more than females but have not provided an explanation for this.

CONCLUSIONS

We could not find evidence for avoidance of power line ROW but constructing roads through forests could be a source of disturbance for moose. Yet seasonal responses indicate that moose, in particular males, are able to tolerate potential disturbance when nearby habitats, even if they provide little cover, warrant utilization. This may be the case for agricultural land during summer and autumn, high productivity forests or when power line ROW and road edges offer feeding opportunities at lower elevations during winter. Female moose appear to be more sensitive to potential disturbance by roads in times of raising young but overall moose seem less sensitive to human linear infrastructure compared to wild reindeer (Vistnes and Nellemann 2001, Vistnes et al. 2004, Kumpula et al. 2007). Our study points towards potential benefits of power line ROW as browsing areas for moose in winter.

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TABLES

Table 1. Ranking of candidate models and model weights according to QIC differences from the top model for each season. “x” signifies first order interactions. Habitat was included as a factor. All other, continuous, variables were modeled including non-linear effects using restricted cubic splines. ”n” indicates the number of observed moose steps. “df” are degrees of freedom.

Model	**df**	**All seasons** (n= 174,765)
m7	26	elevation + habitat × distance to road + habitat x distance to power line
m6	18	elevation + habitat × distance to road + distance to power line
m5	16	elevation + habitat × distance to power line
m4	8	elevation + habitat + distance to power line
m3	16	elevation + habitat × distance to road
m2	8	elevation + habitat + distance to road
m1	6	elevation + habitat

Spring (n=32,972)			**Summer** (n= 31,140)		
Model	**ΔQIC**	**Model weight**	**Model**	**ΔQIC**	**Model weight**
m3	0	0.68	m2	0	0.94
m6	2	0.32	m4	7	0.03
m2	15	0.00	m6	8	0.02
m1	16	0.00	m1	10	0.01
m4	18	0.00	m3	11	0.00
m7	26	0.00	m5	18	0.00
m5	44	0.00	m7	20	0.00

Autumn (n=47,520)			**Winter** (n=63,133)		
Model	**ΔQIC**	**Model weight**	**Model**	**ΔQIC**	**Model weight**
m7	0	1	m4	0	0.98
m3	21	0	m6	10	0.01
m6	26	0	m1	10	0.01
m2	127	0	m2	14	0.00
m5	139	0	m5	15	0.00
m1	144	0	m3	22	0.00
m4	149	0	m7	22	0.00

FIGURES

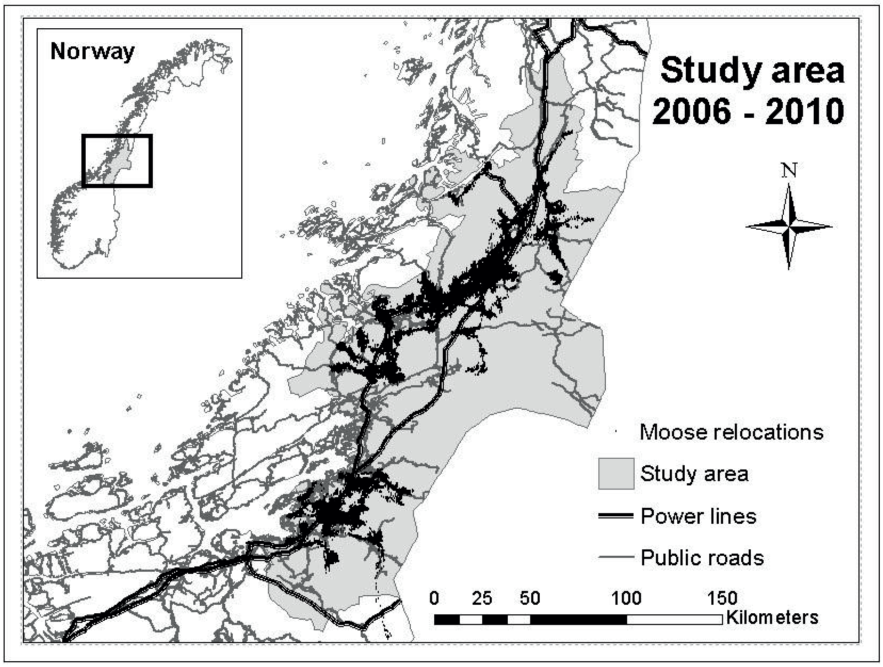

Fig. 1 Study area with moose relocations (black dots), high-voltage power lines (thick black lines) and public roads (grey lines) in central Norway. The 58 individual moose used in the analysis were captured and equipped with GPS collars within the county of Nord-Trøndelag and adjacent areas.

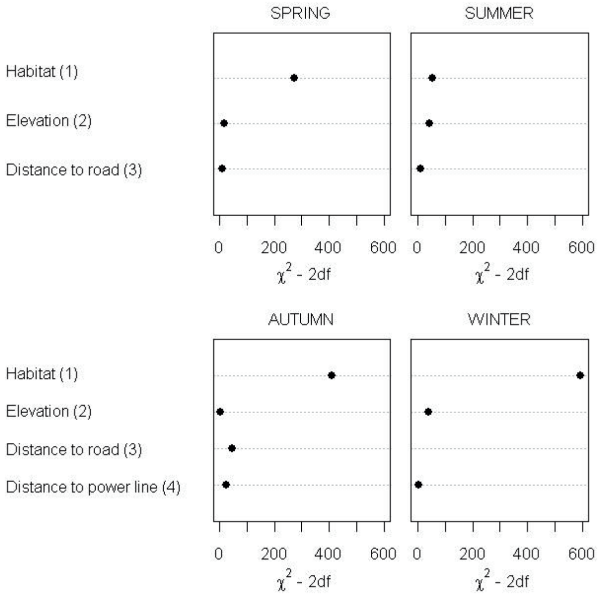

Fig. 2 Importance of variables as indicated in the most parsimonious model based on GPS data from 58 radio-collared moose in the county of Nord-Trøndelag, Norway. The penalized Wald statistics are given of individual variables including their main effects as well as interaction terms with other variables where applicable (1, 3, 4). The penalized Wald statistics are shown for spring, summer, autumn and winter separately. The penalized Wald statistic was calculated from the Wald statistic minus twice the degrees of freedom.

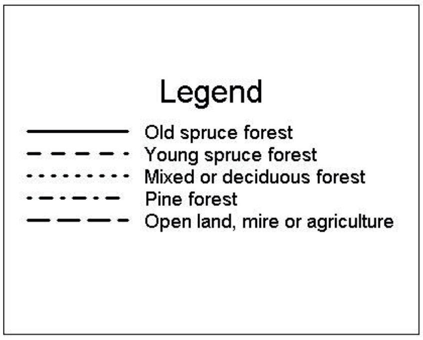

Fig. 3 Legend

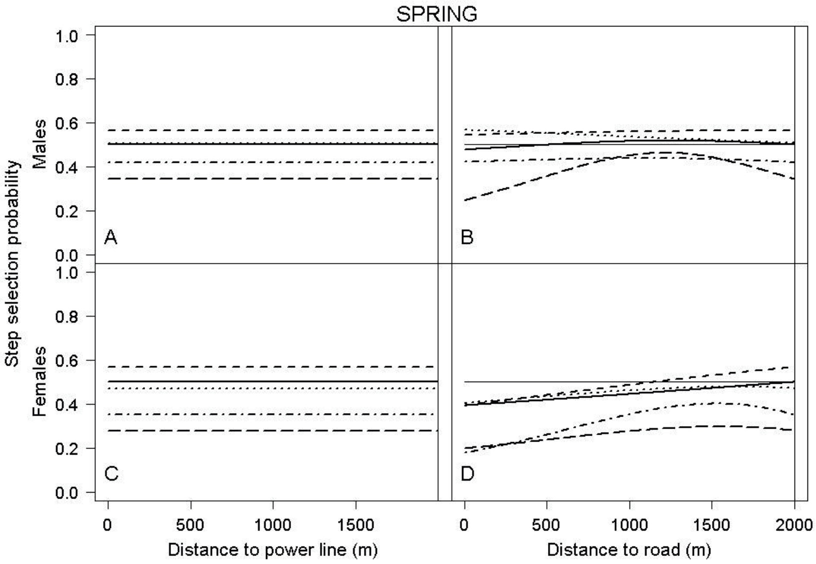

Fig. 3 A – D Step selection probabilities as a function of distance to central-grid power line or distance to road is shown in spring (A - D), summer (E - H), autumn (J - L) and winter (M - P). Step selection probabilities for different gender and habitat types and are indicated. GPS relocation data was obtained from 58 radio-collared moose in the county of Nord-Trøndelag, Norway.

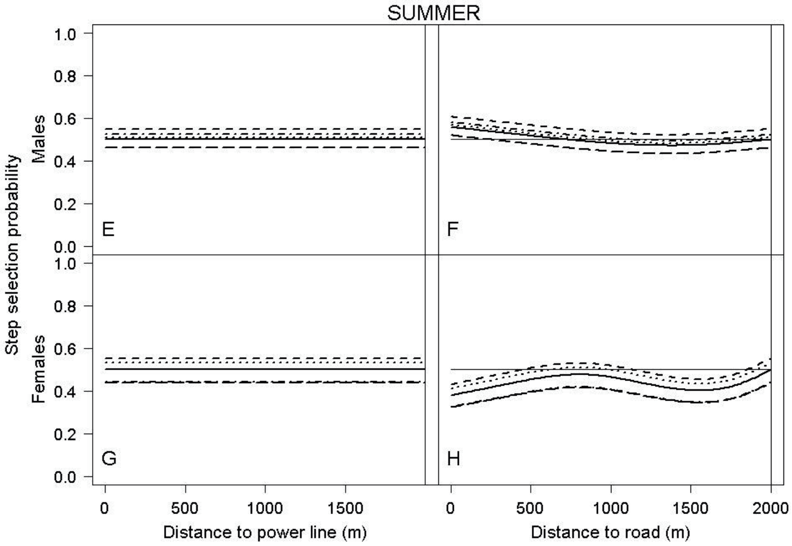

Fig. 3 E – H Description as in **Fig. 3 A - D.**

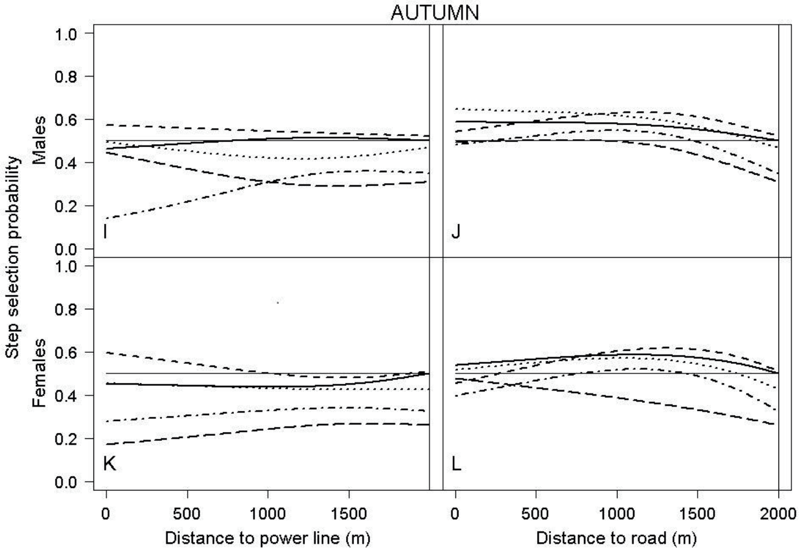

Fig. 3 I – L Description as in **Fig. 3 A - D.**

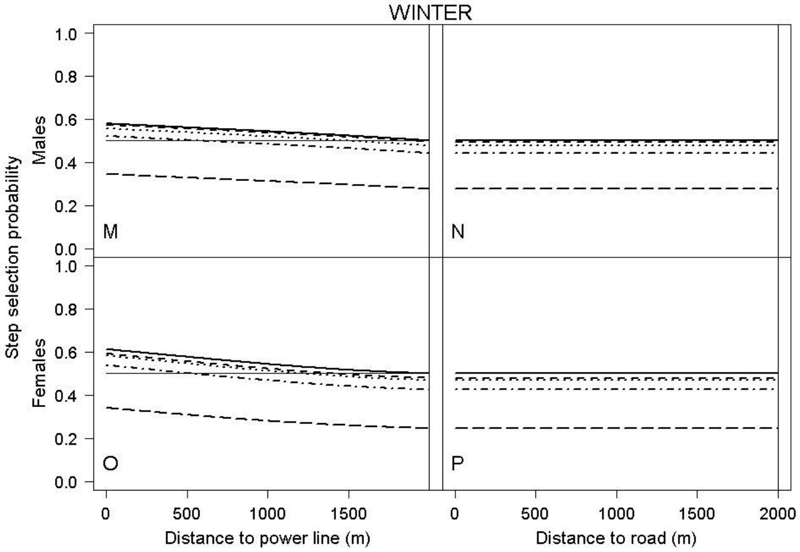

Fig. 3 M – P Description as in **Fig. 3 A - D.**

Appendix

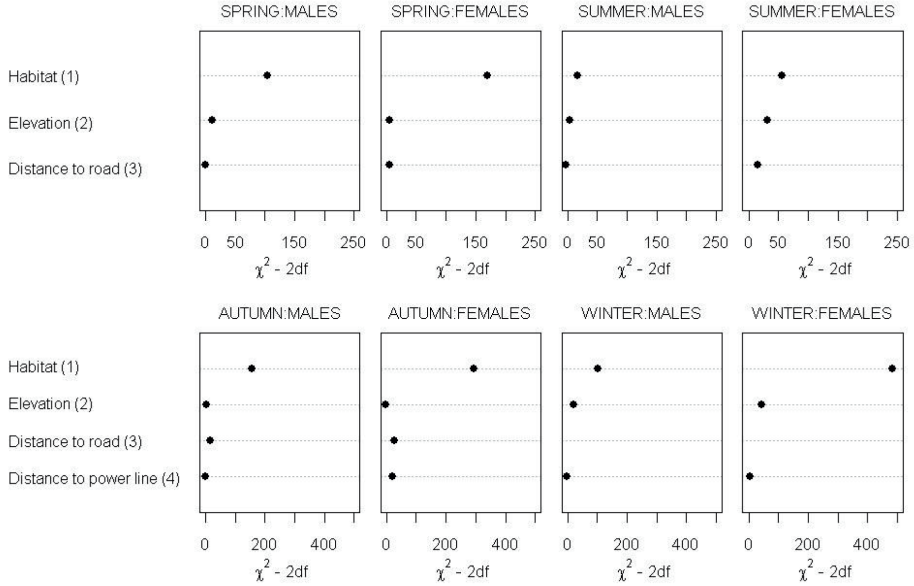

Fig. 1 Importance of variables as indicated in the most parsimonious model based on GPS data from 58 radio-collared moose in the county of Nord-Trøndelag, Norway. The penalized Wald statistics are given of individual variables including their main effects as well as interaction terms with other variables where applicable (1, 3, 4). The penalized Wald statistics are shown for males and females in spring, summer, autumn and winter separately. The penalized Wald statistic was calculated from the Wald statistic minus twice the degrees of freedom.

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Paper II

Paper III

Is not included due to copyright

Paper IV

A review on the effects of power lines on ungulates and its implications for power line routing and rights-of-way management

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Abstract

Thousands of kilometers of power lines exist and more are planned to be built. In Norway, the length of the power line network is similar to that of the road network. Mobile ungulates that range over large areas are likely to encounter power lines, but a synthesis on power line effects on ungulates is lacking. Reindeer *(Rangifer tarandus tarandus)* are suspected to avoid power lines up to distances of 4 km. In contrast, some forest ungulates were shown to preferentially forage in power line rights-of-way (ROWs), cleared areas under power lines. We reviewed the factors that possibly influence avoidance and attraction effects of power lines on ungulates, set into a conceptual framework, and made suggestions on how to mitigate avoidance effects through power line routing and management.

The power line construction and associated noise and electromagnetic fields are possible sources of behavioral disturbance, while rights-of-way management influences the use of the habitat under power lines. Disturbance and altered habitat use can induce barrier and corridor effects, thereby influencing connectivity. Species-specific effects can further determine behavioral disturbance and habitat use. From the reviewed literature, we found little evidence for behavioral disturbance of reindeer or forest ungulates under power lines. Forest ungulates could benefit from browsing opportunities in cleared areas under power lines if they are managed to provide abundant and preferred forage as well as sufficient cover. However, power lines may facilitate access for hunters and predators. As a precaution, construction of power lines should be avoided in areas and during times of calving.

More research is needed to find out if power lines increase avoidance and barrier effects of other human features, and how the width of the ROW corridor may influence ROW crossings and edge effects. To establish a causal relationship between the construction of power lines and potential avoidance, before-after-impact-control studies are recommended. Differences in the sensitivity of reindeer dependent on their degree of domestication may be expected.

Keywords: power lines, rights-of-way, ungulates, disturbance

Introduction

The transmission network for power lines of at least 220 kV covers circa 300,000 km in Europe (European Network of Transmission System Operators for Electricity 2012) and 250,000 km in the USA (Abraham 2002). However, power lines above 220 kV may only constitute a small proportion of the total grid. Circa 200,000 and 450,000 km of overhead power lines carrying various voltages exist in Norway (Statistics Norway 2011) and Sweden (Grusell and Miliander 2004) respectively.

In Norway, the total length of the central power line grid is only half of the central road network (28,000 km versus 55,000 km, **Appendix A**), but it ties up over 20% more surface area due to required corridor widths (740 km^2 versus 630 km^2, **Appendix A**). The footprints of the distribution power line grid and road network are similar (**Appendix A**). The Norwegian central grid operator Statnett is planning to increase the construction of power lines to 300 km per year by 2020 (Statnett SF 2013). 3,500 – 4,500 kilometers of new power lines are planned in Germany until 2022 (Feix et al. 2012). We estimated that over 60 % of central grid power lines in Norway traverse forests, while circa 40 % of the land area is covered by forest (**Appendix B, Table 2**).

An extensive body of research documentation on potential effects of roads on wildlife is available (reviewed in: Forman and Alexander (1998), Spellerberg (1998), Seiler (2001), Fahrig and Rytwinski (2009), Coffin (2007), Benitez-Lopez et al. (2010)), but the knowledge on power line effects is scattered. Similar to roads, power lines may influence wildlife species in a variety of ways through disturbance, clearing of forest habitat under power lines, edge, barrier and corridor effects (Willyard and Tikalsky 2004, Ball 2012). Fragmentation could induce genetic drift, as for roads (Epps et al. 2005, Kuehn et al. 2007), and reduce population productivity and persistence (Griffen and Drake 2008, Haanes et al. 2013). Wide-ranging and mobile species as some ungulates will likely encounter power lines within their home ranges.

If disturbance by power lines is analogous to predation risk, it can cost energy for fleeing, increased vigilance, lost resources in habitats associated with danger and impaired mating and parental investment (Frid and Dill 2002). Should ungulates by disturbed by power lines, they can be expected avoid power lines to reduce these costs.

However, cleared areas under power lines turn into early- to mid-successional habitats (Bramble and Byrnes 1982) and provide benefits through additional browse for forest ungulates (Bramble and Byrnes 1972). This may results in attraction effects towards power line ROWs.

The aim of this article is specifically to review the factors that possibly influence avoidance and attraction effects of power lines on ungulates (**Appendix C**), set into a conceptual framework (**Figure 1**). Research has been undertaken on reindeer in open alpine areas in Norway and on other ungulates in forests in Canada, USA (**Appendix C**) and Norway (Bartzke et al. in press).

We identified proximate and ultimate causes of avoidance and attraction effects resulting from power line routing, construction, rights-of-way management and species-specific effects. The power line construction may induce behavioral disturbance. Rights-of-way management and routing is expected to influence the use of the ROW habitat. Sensitivity to disturbance and habitat preferences, which are influenced by species-specific effects, should further affect behavioral disturbance and habitat use. Both habitat use and behavioral disturbance influence avoidance and attraction effect. Therefore, power line routes could function as barriers and/or corridors with consequences for connectivity and induce functional loss of habitats. Finally, we suggest how to mitigate avoidance effects through power line routing and ROW vegetation management.

Behavioral disturbance from power line constructions

Power lines could disturb ungulates because they are artificial structures that emit noise and electromagnetic fields. Frid and Dill (2002) synthesized that disturbance should be analogous to predation risk. When disturbed, ungulates may spend more time vigilant (Loehr et al. 2005, Benhaiem et al. 2008, Crosmary et al. 2012), leaving less time for vital activities like feeding (Underwood 1982, Childress and Lung 2003, Fortin et al. 2004, Colman et al. 2012). Reproductive behavior can be impaired (Clair and Forrest 2009). Flight behavior costs energy (Cassirer et al. 1992, Bradshaw et al. 1998, Rumble et al. 2005).

Noise

Electrical discharge by power lines produces crackling or hissing corona noise (Straumann 2011). Wind can produce Aeolian noise though vibrations of the physical structure (Tsujimoto et al. 1991). An audiogram suggests that reindeer are able to hear corona noise from power lines (300 and 420 kV) up to distances of 79 m (Flydal et al. 2010). Noise of the intensity of an aircraft increased heart rates and alerted or alarmed dessert ungulates (Weisenberger et al. 1996). However, noise of a 500 kV transmission line did not influence cattle behavior (Ganskopp et al. 1991).

Electromagnetic fields

Power line electromagnetic fields are suspected to disturb the hypothesized magnetic alignment of cattle and roe deer (*Capreolus capreolus*) (Burda et al. 2009). However, ungulates may align themselves in the direction of power lines (Fig. 1, 2 in Burda et al. (2009)), supposedly interrupted in their north south alignment (Begall et al. 2008), for other reasons that were not accounted for. Fluctuations in electric fields of a 500 kV power line did not influence cattle behavior (Ganskopp et al. 1991). Domestic-tame reindeer in enclosures became more restless and moved further away from power lines (132 and 300 kV) when transmission load increased but the same was observed for control groups (Flydal et al. 2009).

Other responses

The visual distraction of power lines in the absence of noise and electromagnetic fields has, as far as we found, not been tested. The lack of behavioral disturbance under power lines in general may however indicate that the sight of power lines was not a source of disturbance. Domestic-wild reindeer in enclosures stayed away from power lines (132 and 300 kV) in the beginning of the study period but the same observation was made for control groups (Flydal et al. 2009). Domestic wild reindeer were more restless than domestic tame reindeer. However, control animals became more restless than treatment animals over time, indicating that power lines were not the source of restless behavior. Deer (*Odocoileus* spp.), elk (*Cervus canandensis* spp.) and other ungulates fed in a power line ROW (500 kV, 41 m wide) without signs of disturbance apart from a five minute motionless period when entering the ROW (Goodwin Jr (1975)).

White-tailed deer (*Odocoileus virginianus*) (Bramble and Byrnes 1972, Doucet et al. 1983), moose (*Alces alces*) (unpublished data), bighorn sheep (*Ovis canadensis canadensis*) and elk (Goodwin Jr 1975) bedded under power lines. Feeding positions and activity of cattle were similar in pens with and without power lines (Ganskopp et al. 1991). Other studies indicate that the vegetation in power line ROWs rather than disturbance by power lines influence the use of those areas by ungulates (Goodwin Jr 1975, Morhardt et al. 1984).

Reimers and Colman (2009) concluded from a literature review that human activities have brief and moderate effects on the behavior and physiology on reindeer and caribou (*Rangifer tarandus*). Energy spent in response to indifferent stimuli may be wasted (Reimers and Colman 2009). Although the given examples provide little evidence for the disturbance of ungulate behavior by power lines, it does not necessarily mean that ungulates are not impacted by power lines. Human disturbance increased cardiac rates of bighorn sheep without changing their behavior (MacArthur et al. 1979, MacArthur et al. 1982). Chronic stress can have adverse effects on reproductive, immune and neural systems and suppress growth in the absence of behavioral changes (Wingfield et al. 1997).

Altered habitat use at power line rights-of-way

Displacement from rights-of-way

Besides possible disturbance effects of power lines, forest ungulates may be displaced from cleared habitats under power lines because they lack canopy cover (Rieucau et al. 2007) and forage in the first years after clearing (Bramble and Byrnes 1982, Lamothe and Dupuy 1984, Ricard and Doucet 1999, Hydro Québec 2013). Moose frequented power line ROWs (220 and 735 kV; 90 – 140 m wide) less than control forests at 2 km distance, and displacement increased where vegetation treatment reduced forage (Joyal et al. 1984). White-tailed deer used a power line ROW (735 kV, 150 m wide) cleared two years before the study significantly less than adjacent forest, indicated by pellet group counts (Lamothe and Dupuy 1984). The cleared areas were also used less than wooded strips inside the ROW. White-tailed deer abandoned more food provided in feeders inside a power line ROW (30 m wide) and along the ROW edge compared to adjacent forest edge and forest at 15 – 30 meter distance from the edge apparently because of the lack of cover (Rieucau et al. 2007).

These results indicate that forest ungulates may be displaced by power line ROWs when food and cover are lacking.

Rights-of-way as novel habitat

Following regrowth, habitats in power line ROWs can, however, also create novel habitats for forest ungulates through the provision of attractive feeding opportunities (Bramble and Byrnes 1979, Lamothe and Dupuy 1984, Ricard and Doucet 1999, Hydro Québec 2013). Over a three year period, Bramble and Byrnes (1972) found more pellets of white-tailed deer in a 40 m wide power line ROW, that was cleared 15 years before the study, compared to the edge of the ROW. The ROW provided more forage and was browsed more intensely compared to forest at 10 m distance from the edge. White-tailed deer frequented a recently cleared 30 m wide power line ROW more than a forested area (Cavanagh et al. 1976). In contrast to the ROW, the forest contained no stems that were browsed. Black-tailed deer (*Odocoileus hemionus columbianus*) used a power line ROW significantly more than adjacent mature forest (Loft and Menke 1984). Deer use increased with shrub and herbaceous cover as well as foraging plants. These results indicate that food availability in power line ROW habitat is important for the use of that habitat by forest ungulates.

Not only the amount of forage, but also its composition may influence the use of power line ROWs for browsing (Milligan and Koricheva 2013). Moose browsed seven times more intensely in power line ROWs compared to forests at two km distance despite the overall lower availability forage (Ricard and Doucet 1999). The ROWs contained seven times more preferred willow stems (*Salix* spp.). White-tailed deer browsed more intensely in three of four sites in a ROW (twin power lines, 735 kV, 150 m wide) compared to lateral forest, even though those sites contained fewer twigs (Lamothe and Dupuy 1984). Possibly the proportion of preferred forage had an influence. Browsing intensity in a power line ROW site by white-tailed deer dropped from circa 35% to circa 6 % after the increase of intolerant species despite an increase in twig availability (Garant et al. 1987). The intensity of browsing by white-tailed deer inside power line ROWs appeared to vary dependent on the proportion of preferred stems rather than total stem availability (Mayer 1976). It seems that not only forage quantity but also composition determines the use of power line ROW for browsing.

Trees that have been cut could provide higher quality browse because they should prioritize growth instead of defense against herbivore damage through secondary metabolites (Rea and Gillingham 2001). However, the increased availability of light in power line ROW clearings may promote both growth and defense (Nybakken et al. 2013). Herbs growing in a power line ROW provided higher concentrations of protein and minerals and contained less fiber compared to woody browse (Bramble and Byrnes 1972). The quality of the forage can be expected to influence the attractiveness of power line ROW habitat for forest ungulates.

Edge habitat along rights-of-way

Forest ungulates can benefit from the increased availability of shrubs not only inside power line ROWs but also along edges (Bramble and Byrnes 1979). Lamothe and Dupuy (1984) noted more white-tailed deer tracks along the edge of a power line ROW (twin power lines, 735 kV, 150 m wide) compared to the ROW and lateral forest. However, fewer pellets were found in the ecotone between cleared areas and lateral forest compared to further inside the forest (Lamothe and Dupuy 1984), indicating that deer may have spent more time in areas of better cover.

Rieucau et al. (2007) noted an increased availability of stems within 3 m from a 30 m wide power line ROW edge compared to the ROW and forest at 15-30 m distance from the ROW. Stem density was elevated up to 5 m from a 30 m wide power line ROW compared to further inside deciduous forests (Powell and Lindquist 2011). Forest within 10 m from a 15 – 30 m wide power line ROW contained more stems below 10 cm diameter than forest at a further distance (Luken et al. (1991, 1992)). 18 of 20 shrub species were significantly more likely to be found at the edge of a 60 m wide power line ROW compared to its center (Brisson et al. 1997). Shrub availability along power line ROW edges may favor ungulate browsing and habitat use along those edges but a link between the two has, as far as we found, not been established.

Functional loss of habitat

Disturbance by power lines may not only affect the use of areas directly under power lines but also habitats adjacent to it. Panzacchi et al. (2013) compared current to historic area use of wild reindeer.

Power lines contributed to a reduction in area use of wild female reindeer within 1 km from pitfall traps and hunting blinds. The density of semi-domesticated reindeer was 73 % lower closer than 4 km from a power line (132 kV) than further away during calving in areas of rugged terrain (Vistnes and Nellemann 2001). However, more favorable snow conditions and lower predation rates at higher elevations further away from power lines may have influenced this result (Reimers and Colman 2009). Reimers and Colman (2009) reported that semi-domesticated reindeer migrated towards a fence at higher elevations despite snowmobile herding close to the fence while human traffic closer to the power line was low.

Nellemann et al. (2001) observed that wild reindeer used areas within 2.5 km from power lines (300 and 420 kV) less than expected in six of eight sampling years. Vistnes et al. (2001) used the same dataset and found that wild reindeer used areas transected by power lines less than expected. However, the accessibility of lichen forage, provided by an index of snow depth and hardness, was approximately three times lower in areas transected by power lines and other infrastructure (Vistnes et al. 2001). The influence of forage accessibility, although not significantly different between areas, could be discussed. Wild reindeer became less abundant in areas within 4 km from power lines (300 and 420 kV) or roads after they were built and more abundant in areas above this distance (Nellemann et al. 2003). However, the shift in abundance coincides with the flooding of an area close to power lines and roads following the construction of a dam (Fig. 3, 4 in Nellemann et al. (2003)).

In contrast, counts of wild reindeer were disproportionately high within 5 km from power lines and minor roads above 1,400 m a.s.l in summer (Vistnes et al. 2008). There was no clear evidence for aversion effects by wild reindeer along a 66 kV power line indicated by lichen measurements (Reimers et al. 2007). Moose did not avoid moving towards central grid power lines except in certain habitats during autumn (Bartzke et al. in press). Hydro Québec (2013) reported that the use of winter feeding grounds by white-tailed deer was not inhibited by power line ROW (120 – 735 kV, 30 – 164 m wide) close to them. There is the possibility that reindeer avoided areas close to power lines because they were disturbed by power lines, but confounding factors may have had an influence.

Connectivity and power line routing

Power line routes as barriers

Disturbance by power lines and the lack of canopy cover in power line ROWs may prevent animals from crossing power lines. Vistnes et al. (2004) concluded that wild reindeer refrain from crossing power lines based on lichen measurements on two sides of parallel power lines (132 and 300 kV) indicating differential grazing. However, these power lines were routed along a dam in the northern part of the study area that could have impeded crossings. The side that was apparently less grazed in the southern part of the study area was closer to a main road and urban settlements at lower elevations. Reimers et al. (2007) suggested that harvesting along a summer open road along power lines could have been another alternative explanation for reduced area use. Wild reindeer crossed a 66 kV power line in 14 of 22 years according to aerial surveys (Reimers et al. 2007).

Bergerud et al. (1984) reviewed movements of eight caribou populations, including a wild reindeer population in Norway, and concluded that caribou cross major transportation corridors unless populations declined and ranges contracted. Strand et al. (2001) hypothesized that wild reindeer cross barriers when the need to migrate is extra large based on the difference in the availability and accessibility of forage, disturbances, predation risk and distance between alternative feeding areas.

Moose did not refrain from crossing central grid power lines (Bartzke et al. (unpublished data)) or power line (735 kV) ROWs that were 90 m wide (Joyal et al. 1984). Neither did white-tailed deer refrain from crossing power line (120 – 735 kV) ROWs of 30 – 146 m width (Hydro Québec 2013). Goodwin Jr (1975) followed 87 elk and nine deer (*Odocoileus spp.)* and observed that only two animals failed to cross a power line ROW (500 kV, 41 m wide). However, white-tailed deer reduced crossings away from a planted area within a power line ROW (120 kV, 30 m wide) (Doucet et al. 1983). Moose refrained from crossing power line (230 – 735 kV) ROWs that were 140 m wide (Joyal et al. 1984). The need to cross power lines, the size of the power line construction, transmission load, the width of the corridor and the availability of cover may influence the willingness of ungulates to cross power lines.

Power line routes as corridors

Increased food availability along forest edges or routes for easy travel may encourage movement of ungulates along power lines. Moose increased movements along central grid power lines over movements towards and away from power lines when getting closer (Bartzke at al., unpublished data). However, when close enough to cross power lines, moose were moving randomly with respect to the power line. Goodwin Jr (1975) observed an elk (*Cervus canandensis*) cow with two calves travelling about 275 meters along a power line ROW (500 kV, 41 m). Forman and Deblinger (2000) sighted a moose that travelled along a power line ROW and a railroad. We found no further evidence for the use of power line ROWs as movement corridors. However, moose (Bartzke et al., unpublished data) and bison (*Bison bison*) (Bjornlie and Garrott 2001, Bruggeman et al. 2007) were shown to move along roads, although surrounding terrain (Bruggeman et al. 2006) and forest cover (Bartzke et al., unpublished data) can be confounding.

Species-specific ultimate and proximate causes

Sociality

Reindeer in Norway may in general be more sensitive to power lines than other ungulates like moose or white-tailed deer because they live in large groups in open alpine habitat experiencing comparatively low human use but intense seasonal hunting. These attributes were shown to increase ungulate flight responses (Stankowich 2008). In open habitats, ungulates should detect and react to disturbances at greater distances because there are no escape habitats to seek refuge (Stankowich 2008). In theory, reindeer in larger groups may spend more time being disturbed because they have a greater chance of detecting disturbances (Taraborelli et al. (2012) for guanaco's (*Lama guanicoe*)), and disturbance might be transmitted between group members (Stankowich 2008).

Groups of West Greenland caribou (*Rangifer tarandus groenlandicus/tarandus*) became aware of humans at larger distances than solitary individuals (Aastrup 2000). Feral reindeer fled at shorter distances to humans in larger groups (Reimers et al. 2006). Although larger groups of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) did not discover observers earlier, they were reported to correspond cooperatively (Colman et al. 2001).

This could be an evolutionary advantage for the detection of real predators but a disadvantage if the source of the disturbance is not lethal. Then animals loose time and energy in being unnecessarily disturbed. The degree of reindeer domestication may also influence their sensitivity to disturbance (Flydal et al. 2009, Reimers et al. 2012).

Life history and mobility

In contrast to reindeer, solitary moose or white-tailed deer traversing forests may not become aware of the presence of power lines until they approach the open corridor, unless they have memorized the location of the power line. Stationary animals (Ramanzin et al. 2007, Bunnefeld et al. 2011), especially those with smaller home ranges, may not come close enough to power lines to be able to respond to them.

Another possible explanation for the lack of power line avoidance by forest ungulates is that animals don't have alternative habitats available, or that the costs of reaching those habitats outweigh the costs of remaining close to power lines (Gill et al. 2001). This could occur in times or areas of resource limitations. White-tailed deer increased stationary browsing time in a power line ROW from ~7 to ~40 % in a cold winter compared to a mild winter (Doucet et al. 1987). Possibly forest ungulates cannot afford to avoid power line ROWs when overall food availability is insufficient in relation to their densities (Ytrehus et al. 1999, Lamoureux et al. 2001). Hagen et al. (2007) speculated that reindeer will also react less to disturbances when the population size increases.

Gender

Several, although not all (Frid 2003, Mahoney et al. 2011), studies indicate that groups with calves (Aastrup 2000), females with young (Ciuti et al. 2008) and females in times of calving or raising calves (Maier et al. 1998, Vistnes and Nellemann 2001, Bartzke et al. in press) are most sensitive to human disturbance (Wolfe et al. 2000). However, we found no clear evidence for gender-specific effects towards power lines (Vistnes and Nellemann 2001, Bartzke et al. in press). Possibly power lines are not disturbing enough to promote gender-specific effects in contrast do direct harassment by humans or motorized vehicles.

Potential demographic impacts

An increased rate of disturbance in connection with an increased rate of predator encounters can result in a reduction of population size (Frid and Dill 2002) due to increased antipredator investment (stress) (Ydenberg and Dill 1986, Cassirer et al. 1992, Maier et al. 1998, Rumble et al. 2005), reduced net energy intake (Stockwell et al. 1991) and body condition (Bradshaw et al. 1998, Luick et al. 2011). Fragmentation effects could contribute to a population decline (Nellemann et al. 2003), impair migration (Vistnes et al. 2004) and induce genetic drift, as for roads (Epps et al. 2005, Kuehn et al. 2007). Yet we found no evidence that the construction of power lines alone influenced population dynamics of ungulates.

Although power line ROWs can provide additional forage, they could also be an "ecological trap" (Battin 2004). Ecological traps are thought to occur when the attractiveness of a habitat (i.e. through increased browse) increases disproportionately relative to its value for survival and reproduction. Power line ROWs along with access roads may provide access for hunters (Goodwin Jr 1975, Perry et al. 1997). Natural predators were reported to travel along power line ROWs (Foster (1956) in Ball (2012), Paquet et al. (1996), Gurarie et al. (2011)). Power lines provide nesting and perching opportunities for the golden eagle (*Aquila chrysaetos*) (Steenhof et al. 1993, Prather and Messmer 2010, Nadjafzadeh et al. 2013), which predates on ungulates (Nybakk et al. 2002, Norberg et al. 2006, Johnsen et al. 2007, Hamel and Côté 2009, Nadjafzadeh et al. 2013). Predation, disturbance and fragmentation induced by power lines could contribute to a population decline. The availability of forage in power line ROWs may favor forest ungulate populations locally.

Knowledge gaps

A causal relationship between the construction of power lines and avoidance by ungulates may be established from before-after impact-control studies (Beyers 1998). A number of the reviewed studies lacked statistical analyses (Bramble and Byrnes 1972, Cavanagh et al. 1976, Mayer 1976, Doucet et al. 1983, Doucet et al. 1987, Garant et al. 1987), did not precisely report the methodology (Loft and Menke 1984), power line voltage and/or ROW width (Ricard and Doucet 1999, Rieucau et al. 2007, Burda et al. 2009, Panzacchi et al. 2013).

There were also large differences in scale ranging from very few meters (Lamothe and Dupuy 1984, Rieucau et al. 2007) up to several kilometers (Vistnes and Nellemann 2001). The scale may however invert the conclusions (Vistnes and Nellemann 2008). The ability to see or hear power lines may be an important factor to be considered, as for roads (Montgomery et al. 2012).

Observing wild ungulate behavior under power lines compared to similar control areas would be necessary to find out if their behavior is disturbed by power lines. Wildlife cameras (Dunne and Quinn 2009, Kuijper et al. 2009) or GPS collars with cameras can be used for this purpose. To separate the causes of possible disturbance, it would be necessary to compare behavior under electrified and non-electrified power lines in warm and windless conditions for electromagnetic fields, different sized non-electrified power lines for visual distraction and to compare behavior in dry and moist weather under electrified power lines for corona noise. Separating the effects of Aeolian noise from wind and visual distraction is not straightforward.

Ideally, experimental and control animal populations should be established. Measuring fecal glucocorticoid concentrations possibly in combination with other disturbance indicators (Tarlow and Blumstein 2007) could help to find out if power lines are anthropogenic stressors. Experiments using reindeer with different degree of domestication should be made as in Flydal et al. (2009).

To better understand barrier and avoidance effects of power line ROWs on forest ungulates, studies examining the effects of ROW width, power line size and voltage, as well as food and cover availability inside ROWs and adjacent forest on power line ROW use and crossings would be useful. Whether resource limitations influence power line avoidance could by tested by comparing responses in areas or times of differing food availability in relation to ungulate density.

Further studies are required to find optimal vegetation management techniques. Experimental studies on the management of power line ROWs have been undertaken in the USA, where the application of herbicides appears to be a common practice to reduce tree regrowth (Cavanagh et al. 1976, Mayer 1976, Bramble and Byrnes 1982, Ballard et al. 2002, Haggie et al. 2008). But this may not be an option in other countries.

Knowledge about the extent of edge effects dependent on ROW width and surrounding forest habitat would help to understand if forest edges created by power line ROWs provide additional feeding habitat for forest ungulates. Knowledge about the preference of human and natural predators for hunting near power lines would be necessary to understand if ungulate populations may be impacted by increased hunting close to power lines.

Routing power lines along existing power lines and roads may reduce the fragmentation of ungulate habitat but at the same increase avoidance and barrier effects (**Table 1**). Female wild reindeer reduced area use within 1 km from ancient pitfall traps and hunting bows when accounting for the effects of power lines and roads more than roads or power lines alone (Panzacchi et al. 2013). The food availability in power line ROWs could attract forest ungulates away from roads and railroads, similarly to supplemental feeding (Wood and Wolfe 1988, Andreassen et al. 2005), and reduce vehicle collisions. However, power line ROWs could also attract ungulates or towards areas surrounding roads. Further studies are necessary to make recommendations for the optimal design of power line networks.

Mitigation measures

Implications for power line routing

The reviewed literature suggests that power lines induce minor negative behavioral responses to ungulates. Most benefits from additional food in power line ROWs for forest ungulates may be expected if those are routed through old coniferous forests with little food but good canopy cover (Bjørneraas et al. 2011). Moose browsed four times more intensely in power line ROWs traversing coniferous forests compared to those traversing mixed forests (Ricard and Doucet 1999). When power lines traverse food-rich young, mixed or deciduous forests, the availability of browse may not compensate for the lack of cover (Rieucau et al. 2007).

In contrast to forest ungulates, a number of the reviewed studies suggest that power lines may be disturbing to wild reindeer inhabiting open alpine areas. However, the lack of clear evidence for the disturbance of semi-domestic reindeer behavior in the proximity of power lines (Flydal et al. 2009) and the maximum distance at which reindeer may hear power lines (79 m) (Flydal et al. 2010) indicates that power lines themselves were not necessarily the main cause for the reduced area use close to power lines reported by Vistnes et al. (2001), Nellemann et al. (2001), Nellemann et al. (2003) and Panzacchi et al. (2013).

Earlier, Vistnes et al. (2004) suggested that that building power lines should be avoided in wild reindeer habitats. This recommendation could be debated.

To minimize inference with reproduction, the construction of power lines, which may require the use of helicopters and building access roads, should be avoided in times and areas of calving. Disturbance after the construction of power lines can be minimized by prohibiting hunting, vehicles and pets along them (**Table 1**). Power line noise and magnetic fields can be reduced through engineering solutions (Teich and Weber 2002, Conti et al. 2003, Kalhor and Zunoubi 2005, Semmler et al. 2005).

Implications for power line ROW management

It is possible to provide attractive power line ROW habitat for forest ungulates with appropriate management (Bramble and Byrnes 1972, Cavanagh et al. 1976, Mayer 1976). A stem height of 4 m for birch and 3.5 m for pine may be the optimal size to provide maximum ungulate forage (Kalén and Bergquist 2004). Felling trees that reach heights of five meters may ensure continuous high browse availability without complete removal of cover. The removal of single large trees would also create gaps for the growth of forbs, ferns and bilberry (*Vaccinum myrtillus*), which can be an important part of forest ungulates diet (Hjeljord et al. 1990, Mysterud and Ostbye 1995, Krojerová-Prokešováa et al. 2010). Alternatively, trees could be cut at a height of one meter instead of full removal to shorten the period of low browse availability after clearing. During construction, hinge cutting, i.e. cutting deciduous large trees only half way through, would maintain cover availability and facilitate regrowth of forage (Global Wildlife Management 2013). Less preferred coniferous trees like spruce (*Picea abies*) could be removed entirely in favor of deciduous trees. Stable scrublands were shown to be more resistant to tree invasion potentially reducing the need for clearing (Niering and Goodwin 1974).

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Tables

Table 1 Possible mitigation measures to reduce adverse effects of power lines on ungulates, modified from Wolfe et al. (2000). Disturbances other than power lines are provided when applicable.

Mitigation measure	**Species**	**Reference**
Avoid constructing power lines in ungulate habitat	Semi-domesticated reindeer *(Rangifer tarandus tarandus)*	Vistnes and Nellemann (2001)
	Wild reindeer *(Rangifer tarandus tarandus)*	Nellemann et al. (2001)
		Vistnes et al. (2001)
		Nellemann et al. (2003)
		Vistnes et al. (2004)
		Panzacchi et al. (2013)
	Moose (*Alces alces*)	Joyal et al. (1984)
	White-tailed deer (*Odocoileus virginianus*)	Lamothe and Dupuy (1984)
		Rieucau et al. (2007)
Avoid constructing power lines in areas/times of calving	Wild reindeer *(Rangifer tarandus tarandus)*	Vistnes and Nellemann (2001)

Table 1 (continued)

Mitigation measure	Species	Reference
Route power lines through old coniferous instead of deciduous, mixed or young forests	Moose (*Alces alces*)	Ricard and Doucet (1999)
Increase food and cover availability in power line ROW to reduce avoidance and barrier effects	White-tailed deer (*Odocoileus virginianus*)	Bramble and Byrnes (1972)
		Cavanagh et al. (1976)
		Doucet et al. (1983)
		Rieucau et al. (2007)
	Black-tailed deer (*Odocoileus hemionus columbianus*)	Loft and Menke (1984)
	Moose (*Alces alces*)	Joyal et al. (1984)
Facilitate the growth of preferred browse species	Moose (*Alces alces*)	Ricard and Doucet (1999)
	White-tailed deer (*Odocoileus virginianus*)	Garant et al. (1987)
Route power lines along existing power lines/roads to reduce habitat fragmentation	Ungulates (roads)	Jaeger et al. (2005)

Table 1 (continued)

Mitigation measure	**Species**	**Reference**
Avoid routing power lines along roads/existing power lines to reduce barrier and disturbance effects	Moose (*Alces alces*)	Joyal et al. (1984)
	Wild reindeer *(Rangifer tarandus tarandus)*	Panzacchi et al. (2013)
Minimize power line noise	Desert mule deer (captive) (*Odocoileus hemionus crooki*) Mountain sheep (captive) (*Ovis canadensis mexicana*) (Response to simulated aircraft noise)	Weisenberger et al. (1996)
Minimize electromagnetic fields	Cattle Roe Deer (*Capreolus capreolus*)	Burda et al. (2009)
Prohibit hunting, vehicles, pets along power lines	Caribou (*Rangifer tarandus*) (Transportation corridors)	Bergerud et al. (1984)
	Mule deer (*Odocoileus hemionus*) (Human with/without dog)	Miller et al. (2001)
	Elk (*Cervus elaphus*) (Road traffic)	Clair and Forrest (2009)

Figures

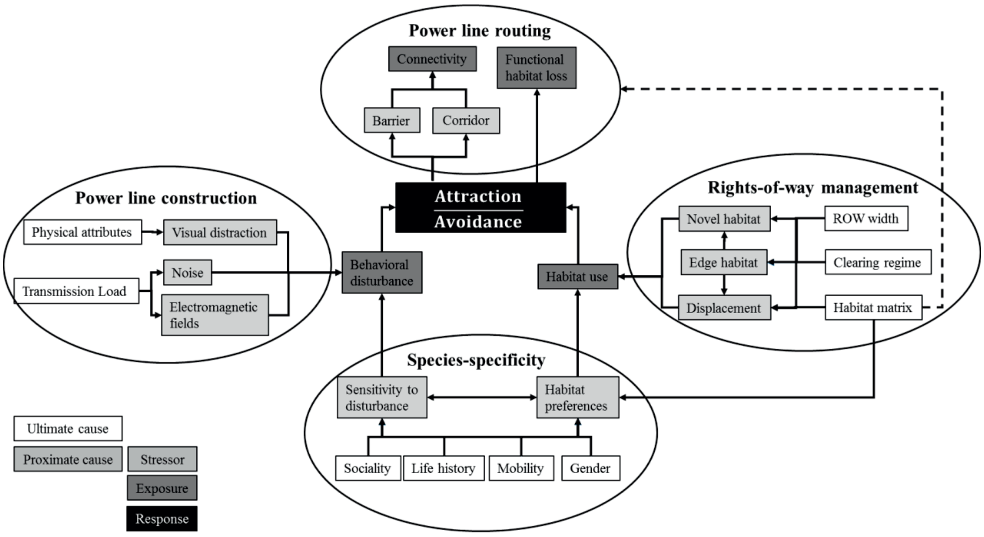

Figure 1 Possible factors influencing avoidance and attraction effects of power lines on ungulates

Appendix A

Land area traversed by power lines and roads in Norway. Line lengths were derived from official statistics (Brunvoll and Monsrud 2011, Statistics Norway 2011a, b). The width of roads consists of road width plus edge. *Lengths were retrieved from a road data base (Norwegian Mapping Authority 2012). Corridor widths are provided following Bevanger and P.G. Thingstad (1988) for power lines and Erik Englien (Statistics Norway, pers. comm.) for roads.

	Type	**Length (km)**	**Corridor width (m)**	**Tied-up surface area (km^2)**
Central power line grid	220 – 420 kV	7,907	38	300
	110 – 145 kV	10,407	25	260
	33 – 66 kV	9,868	18	177
	Total	28,182		738
Distribution power line grid	0.2 – 24 kV	165,789	Variable (ca. 5 – 10)	829 – 1,658
Central road network	Highways	6,639*	17	113
	National roads	20,837*	13	271
	County roads	27,281	9	246
	Total	54,757		630
Distribution road network	Local roads	38,591	8	309
	Private roads	75,453*	7	528
	Forest roads	48,571	7	340
	Total	162,615		1,177

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Appendix B

Method: analysis of power line routing data

We clipped power line routing data from the central grid operator statnett with the contours from the Norwegian land area. We determined the percentage of the line length routed through different habitat types of the norut raster map (Johansen et al. 2009) with the function isectlinerst in the program geospatial modeling environment (Beyer undated). For a comparison, we did the same analysis with data of the central road network (Norwegian Mapping Authority 2012) including highways, national and county roads.

Habitat types were reclassified following **Table 1**. To capture habitats surrounding power lines and roads, we resampled the 30 × 30 m raster to a 60 × 60 m raster. Raster cells that overlapped urban settlement polygons were classified as settlements. The percentage of the different habitat types of the Norwegian land area was the percentage of the respective raster cells. No accurate power line routing data of lower voltage power lines was available. We used ArcGIS version 10 (ESRI 2011) to handle and modify spatial data.

Table 1 Habitat types and their re-classification of the norut vegetation map (Johansen et al. 2009) in Norway

Forest
Dense coniferous woodland
Open coniferous and mixed woodland
Lichen-rich pine woodland
Low-herb woodland and rich deciduous woodland
Tall-herb and tall-fern deciduous woodland
Bilberry and small-fern downy birch woodland
Crowberry downy birch forest
Lichen-rich downy birch forest

Table 1 (continued)

Mire and water
Ombrotrophic hummock bog and lawns
Minerotrophic flat fen
Hollow mire and open swamp
Freshwater
Alpine areas and ridges
Exposed ridges, scree, talus and rock
Gras and wood-rush ridges
Heather ridges
Lichens, heather and pigmy birch
Heather rich lee side
Grass and dwarf willow snow patch
Late snow patch vegetation
Glaciers, permanently snow-covered areas and extreme snow patch plant communities
Grass and heather
Heather and fresh brushwood (lowland and mountain areas)
Herb-rich grassland (lowland and mountain areas)
Agriculture
Towns and villages
Not classified

Table 2 Percentage of central power line and road grid length traversing different habitat types in Norway and the percentage of those habitat types of the land area

Habitat type	Percentage of central grid power line length	Percentage of central grid road length	Percentage of land area
Forest	61	45	39
Grass and heather	11	10	15
Alpine areas and ridges	14	8	31
Mire and water bodies	7	5	11
Agriculture	5	21	3
Settlements	< 1	11	< 1
No data	< 1	< 1	< 1

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Appendix C

Possible of effects of power lines and associated right-of-way clearings on the behavior and area use of ungulates

Effect	**Species**	**Result**	**Reference/ Location of study area**
Disturbance	Cattle Roe deer (*Capreolus capreolus*)	Cattle and roe deer align themselves in the direction of power lines, supposedly interrupted in their north-south alignment.	Burda et al. (2009) Morocco, South Africa, India, Australia, Belgium, Denmark, France, Germany, Ireland, Netherlands, Russia, UK, USA, Argentina
	Semi-domestic reindeer *(Rangifer tarandus tarandus)*	Deer can hear power line (300 and 420 kV) noise up to 79 m distance.	Flydal et al. (2010) Southern Norway
Displacement from rights-of-way	White-tailed deer (*Odocoileus virginianus*)	Significantly fewer pellets were found in cleared areas of a power line ROW (735 kV, 150 m wide) compared to lateral forest.	Lamothe and Dupuy (1984) Eastern Canada

Appendix C (continued)

Effect	**Species**	**Result**	**Reference/ Location of study area**
Displacement from rights-of-way	White-tailed deer (*Odocoileus virginianus*)	Deer left more food inside feeders placed in a power line ROW (30 m wide) compared adjacent forest when regeneration was absent.	Rieucau et al. (2007) Eastern Canada
	Moose (*Alces alces*)	Significantly fewer tracks were found in power line ROW (220 kV and 735 kV; 90 – 140 m wide) compared to transects in forests at two km distance.	Joyal et al. (1984) Eastern Canada
Rights-of-way as novel habitat	White-tailed deer (*Odocoileus virginianus*)	Deer deposited more pellets and browsed more intensely in a power line ROW (40 m wide) compared to the edge of the ROW.	Bramble and Byrnes (1972) North-eastern USA
		More signs of deer use were found inside a newly cleared power line ROW (30 m wide) compared to control forest.	Cavanagh et al. (1976) North-eastern USA
	Moose (*Alces alces*)	Moose browsed seven times more intensely in a power line ROW compared to forests at two km distance.	Ricard and Doucet (1999) Eastern Canada

Appendix C (continued)

Effect	**Species**	**Result**	**Reference/ Location of study area**
Rights-of-way as novel habitat	Black-tailed deer (*Odocoileus hemionus columbianus*)	Deer deposited significantly more pellets inside a power line ROW compared to adjacent mature forest.	Loft and Menke (1984) Western USA
Edge habitat along rights-of-way	White-tailed deer (*Odocoileus virginianus*)	More tracks were found at the edge of a power line ROW (twin power lines, 735 kV, 150 m wide) compared to the ROW and lateral forest.	Lamothe and Dupuy (1984) Eastern Canada
Functional loss of habitat	Semi-domesticated reindeer *(Rangifer tarandus tarandus)*	The density of semi-domesticated reindeer was significantly (73 %) lower below compared to above 4 km from a power line (132 kV) during calving in areas of rugged terrain.	Vistnes and Nellemann (2001) Northern Norway
	Wild reindeer *(Rangifer tarandus tarandus)*	Deer were significantly less abundant than expected in areas within 2.5 km from power lines (300 and 420 kV) in six of eight sampling years.	Nellemann et al. (2001) Southern Norway
		Deer were less abundant in areas transected by power lines (300 and 420 kV) than expected.	Vistnes et al. (2001) South-central Norway

Appendix C (continued)

Effect	**Species**	**Result**	**Reference/ Location of study area**
Functional loss of habitat	Wild reindeer *(Rangifer tarandus tarandus)*	Deer became less abundant (74 %) in areas within 4 km from power lines (300 and 420 kV) or roads after they were built and more abundant in areas above that distance.	Nellemann et al. (2003) South-western Norway
		Power lines contributed to a reduction in area use of female deer within 1 km from pitfall traps and hunting blinds.	Panzacchi et al. (2013) Southern-Norway
Power line routes as barriers	Elk (*Cervus canadensis* spp.) Deer (*Odocoileus spp.)*	Two of 87 elk and nine deer failed to cross a power line ROW (500 kV, 41 m wide).	Goodwin Jr (1975) North-western USA
	Moose (*Alces alces*)	Moose refrained from crossing power line ROW (230 – 735 kV, 140 m wide) significantly.	Joyal et al. (1984) Eastern Canada
	Wild reindeer *(Rangifer tarandus tarandus)*	Significantly different lichen measurements on two sides of parallel power lines (132 and 300 kV) indicated differential grazing on each side.	Vistnes et al. (2004) South-central Norway

Appendix C (continued)

Effect	**Species**	**Result**	**Reference/ Location of study area**
Power line routes as barriers	Wild reindeer *(Rangifer tarandus tarandus)*	Wild reindeer herds crossed a 66 kV power line in 14 of 22 years according to aerial surveys.	Reimers et al. (2007) South central Norway
Power line routes as corridors	Moose (*Alces alces*)	Movements along central grid power lines increased over movements towards and away from power lines when getting closer.	Bartzke at al. (unpublished data) Central Norway
Potential demographic impacts	Wild reindeer *(Rangifer tarandus tarandus)*	Calf/cow ratio declined significantly with the construction of human infrastructure including power lines.	Nellemann et al. (2003) South-western Norway
		89 of 107 hunters said they were hunting in power line ROW or along roads.	Goodwin Jr (1975) North-western USA
		A power line ROW was reported to be a traditionally preferred hunting area.	Perry et al. (1997) Eastern USA

List of errors (corrections are underlined)

Page 19 in thesis summary

Avoidance and attraction effects were defined by a step selection probability below and above 0.5 (**paper I**) or 0.33 (**paper II**) respectively. In **paper I**, the step selection probability was the probability of moving towards linear features. In **paper II**, the step selection probability was the probability of choosing one of three alternative movement steps.

Page 31 in thesis summary

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Page 43 in the thesis summary

[…] University of Wollongong, Wollongong, Australia.

Page 8 in paper I

Males avoided areas below 1 km from roads in open habitats in spring but did not respond strongly to roads otherwise (Fig. 3 B).

Page 10 in paper I

Females in times of raising young appeared to be more disturbed by roads than males.

Page 1, 2 and 10 in paper II

Replace topology with topography

Page 5 in paper II

The study area (64º30'N, 12º50'E, 28,500 km^2) was situated […]

Page 19 in paper II

Effects of movement tactic on components of fitness in a large ungulate - reproductive performance is higher in migratory than in resident female moose 25 pp. *in* The ecological significance of space use and movement patterns of moose in a variable environment. Doctoral thesis. Norwegian University of Science and Technology (NTNU), Trondheim, Norway.

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Page 22 in paper III (table 2)

Model	**ΔAIC**	**~~M3~~weight**

Page 11 in paper IV

Although feral reindeer fled at shorter distances to humans in larger groups (Reimers et al. 2006) and larger groups of Svalbard reindeer […]

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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	The function of bird song in mate attraction and territorial defence, and the importance of song

		Zoology	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.	Breeding strategies in birds: Experiments with the

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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
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1995	Chris Jørgen Jensen	Dr.	The surface electromyographic (EMG) amplitude as

		scient Zoology	an estimate of upper trapezius muscle activity
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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.	Adaptive and incidental biological ice nucleators

		scient Zoology	
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.	A study of driftwood dispersal to the Nordic Seas by

		scient Botany	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.	Biochemical impacts of Cd, Cu and Zn on brown

		scient Zoology	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	Metal binding proteins and antifreeze proteins in the

		Biology	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. Tha 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	Population Ecology of *Eriophorum latifolium*, a

		Biology	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
2011	Simen Pedersen	ph.d Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-	ph.d	Evolutionary consequences of seed banks and seed

	Anbaran	Biology	dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	ph.d Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	ph.d Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	ph.d Biology	Theoretical and empirical approaches to studying foraging decisions: the past and future of behavioural ecology
2012	Aleksander Handå	ph.d Biology	Cultivation of mussels (*Mytilus edulis):*Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	ph.d Biology	Reproductive and migratory challenges inflicted on migrant brown trour (*Salmo trutta* L) in a heavily modified river
2012	Jisca Huisman	ph.d Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	ph.d Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	ph.d Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	ph.d Biology.	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	ph.d Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos.	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	ph.d Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	ph.d Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	ph.d Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	ph.d Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	ph.d Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	ph.d Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	ph.d Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	ph.d Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	ph.d Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	ph.d Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	ph.d Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway

			and Kola Peninsula, NW Russia
2013	Anders Foldvik	ph.d Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	ph.d Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	ph.d Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	ph.d Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Ragnhild Pettersen	ph.d Biology	Identification of marine organisms using chemotaxonomy and hyperspectral imaging
2013	Angela Mwakatobe	ph.d Biology	Human-Wildlife Interaction in the Western Serengeti: Crop Raiding, Livestock Depredation and Bushmeat Utilisation
2013	Nina Blöcher	ph.d Biology	Biofouling in the Norwegian Salmon Farming Industry
2013	Cecilie Miljeteig	ph.d Biology	Phototaxis in Calanusfinmarchicus - light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	ph.d Biology	Molecular and functional characterisation of signalling peptides of the IDA family in *Arabidopsis thaliana*
2013	Marianne Nymark	ph.d Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	ph.d Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	ph.d Biology	Factors influencing African wild dog *(Lycaon pictus***)** habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	ph.d Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	ph.d Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	ph.d Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (***Salmo salar L***.)