Norges miljø- og
biovitenskapelige
universitet

Master's Thesis 2016   60 credits

Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natural Resource Management

Effect of mountain biking on red deer (*Cervus elaphus*) in Kaupanger, Norway

Janneke Scholten
Master in Ecology

ACKNOWLEDGEMENTS

This thesis marks the end of a great and interesting experience. I had the privileged to do my fieldwork in one of the most beautiful parts of Norway and discovered that what you find in the field not always correspond with your plans. It was, therefore, not only a challenge to set up a completely new project, but also to adjust the plan in the field. Furthermore, I gained more statistical knowledge and started even liking the program R. Also my writing skills improved and I deliver this thesis with proud.

I would like to thank my supervisors Stein Ragnar Moe (NMBU) and Stein Joar Hegland (Sogn og Fjordane University College) for their guidance throughout the project, from setting up the project, guiding me through my fieldwork and statistical analysis and giving critical feedback on my writing. Furthermore, I like to thank Richard Bischof (NMBU) for helping me figuring out and understand the most difficult part of my statistics. Many thanks to Arne Glenn Flåten for letting me stay in Vesterland Feriepark during my fieldwork, it was great to be able to take a nice shower and relax in a warm cosy cabin after a day in the field. I am also grateful towards Nils Joachim Knagenhjelm for letting me do research on his land and providing me information about other activities that might affect deer occurrence. Furthermore, I like to thank Aslak Os (Rocketfarm) for providing the map with biking trails and Guttorm Flatabø (Vestlandsforsking) for helping me convert this map into a format I could use, thereby making it possible for me to show my results in a nice and clear way. I like to thank my classmates, especially Marte Olson, for good discussions, support and company during the breaks. Last but not least, I would like to thank my parents and sister for their love and moral support.

Ås, 12 May 2016

Janneke Scholten

ABSTRACT

Human outdoor activities, like mountain biking, often affect animal behaviour. Ungulates might avoid roads and trails, and increase their avoidance with increasing human activity. Recently, biking on forest trails has increased considerably in Norway, but we still have limited knowledge about how forest biking may affect wildlife. In this study, I used pellet group counts and camera traps to study the effect of biking trails on red deer occurrence in Kaupanger, Norway. Based on pellet group counts, red deer avoided biking trails up to 40 m. The camera trap data showed that there was a tendency of a decreased deer occurrence with increasing human activity (trail width) during the day. Furthermore, males reacted stronger to increasing human activity than females. My findings imply that mountain biking has an effect on red deer. A further increase in biking may result in a higher avoidance and, thus, less suitable habitat for red deer in the forest area.

CONTENTS

INTRODUCTION

Activities like hiking, horseback riding, mountain biking and, in the winter, skiing are popular outdoor activities, that often influence wildlife (Davis et al. 2010; Marchand et al. 2014; Naylor et al. 2009). Recreational use may affect animals short-term (flight response) or long-term (distribution, activity patterns, habituation) behavioural patterns, which in turn may affect species physiology, reproduction and physical health (Stankowich 2008).

To facilitate recreation opportunities, people built more cabins, ski resorts and roads. In general, animals tend to avoid such human infrastructure (Jiang et al. 2007; Manor & Saltz 2005; Thiel et al. 2007; Torres et al. 2014; Vistness & Nellemann 2001) and may even adjust their home ranges to avoid disturbance by tourism (Thiel et al. 2007). Tracks and trails used by hikers and bikers also affect wildlife behaviour; animals avoid trails and increase their movement rate close to trails (Arnberger et al. 2008; Belotti et al. 2012; Licoppe & De Crombrugghe 2003; Rogala et al. 2011; Skarin et al. 2010). Furthermore, high levels of human activity may cause higher avoidance of trails (Longshore et al. 2013; Sibbald et al. 2011). Off-trail biking is also common and often affect wildlife on a larger scale than more predictable, on-trail disturbance (Bateman & Fleming 2014; Miller et al. 2001; Stankowich 2008; Taylor & Knight 2003; Wolf & Croft 2010). Habituation may decrease the effect of human disturbance on wildlife (Cassirer et al. 1992; Kloppers et al. 2005; Papouchis et al. 2001; Recarte et al. 1998). Whether ungulates habituate to the disturbance depends on the predictability of the disturbance (Kloppers et al. 2005; Papouchis et al. 2001; Recarte et al. 1998; Reimers & Colman 2006). It is more likely that animals habituate to a predictable disturbance, for example on-trail recreation or a road, then unpredictable disturbance, for example off-trail recreation or hunting (Kloppers et al. 2005; Papouchis et al. 2001; Recarte et al. 1998; Reimers & Colman 2006; Stankowich 2008)

Ungulates show increased vigilance in response to increased disturbance (Borkowski et al. 2006; Brown et al. 2012; Jayakody et al. 2008; Kloppers et al. 2005; Langbein & Putman 1992). This trend in vigilance can decrease the time spent feeding (Frid & Dill 2002; Jayakody et al. 2008) and thus, may affect animal condition. Increased disturbance may increase flushing probability and distance moved, although flushing response often differs between species and type of disturbance (e.g. roads, tracks, hikers, skiers) (Borkowski et al. 2006; Colman et al. 2012; Manor & Saltz 2005; Miller et al. 2001; Naylor et al. 2009; Skarin et al. 2010). For example, mule deer (*Odocoileus hemionus*) responded less to single on-trail hikers compared to an on-trail hiker with a dog on leash and responded most negative to off-trail hikers (with and without dogs) (Miller et al. 2001). Furthermore, elk (*Cervus canadensis*) is more vigilant towards snowmobiles and snow coaches than bison (*Bison bison*) (Borkowski et al. 2006). However, these behaviours not necessary affect the long-term responses (Guillemain et al. 2007).

Long-term response of ungulate disturbance consist of, for example, avoiding the disturbance areas by selecting less disturbed habitats (Alves et al. 2014; Arnberger et al. 2008; Meisingset et al. 2013; Sibbald et al. 2011; Wisdom et al. 2004). In some cases, ungulates adjust their home ranges and increased disturbance may even lead to complete displacement (Laurian et al. 2008; Neumann et al. 2009; Seip et al. 2007). Avoidance of disturbed areas force animals to forage in other places, which may be of lower quality than the area closer to the disturbance and thus, affect their diet (Jayakody et al. 2008). Eventually, living in suboptimal habitat may affect the fitness of the population. However, ungulates respond to fluctuations in the disturbance level and even return to places closer to trails when disturbance is low, implicating that animals may have a trade-off between the amount of disturbance and the food quality close to the trails (Longshore et al. 2013; Rogala et al. 2011).

A maximum avoidance distance to trails can be used to draw an effect zone for recreational trails. The size of the effect zone depends on the species and intensity of the disturbance (Gagnon et al. 2007a). Effect zones for trails vary between 286 m in male red deer (*Cervus elaphus*), in responds to hiking trail with low human disturbance (Sibbald et al. 2011), up to 750 m found in woodland caribou (*Rangifer tarandus caribou*) in response to abandoned roads (Leblond et al. 2011).

Hikers and bikers are most common during periods without snow. Biking may impact vegetation, soil and water quality, but also affect wildlife (Lathrop 2003; Marion & Wimpey 2007; Quinn & Chernoff 2010). Some studies did not find differences in ungulate response between hikers and bikers (George & Crooks 2006; Taylor & Knight 2003), whereas Naylor et al. (2009) found that mountain biking had larger impact on elk behaviour than hiking. In contrast, other studies found that that bicycles were not an important predictor of responsive behaviour and that, in general, humans on foot disturbed ungulates more than mountain bikers or vehicles (Brown et al. 2012; Papouchis et al. 2001; Stankowich 2008). All of these studies on mountain biking are from North America. As far as I know, no similar studies on the effects of mountain biking (or in combination with hiking) have been done on ungulates in Europe.

Mountain biking is rapidly developing in Norway. In this study, I examined the effect of mountain biking on red deer occurrence in Kaupanger, Norway. In Kaupanger, there is almost year-round mountain biking activity. Also hiking and, in the winter, skiing are popular activities. Based on the number of car collisions, the density of red deer is high in the area (Hegland 2012). Mountain biking is still increasing and biking trails are covering a larger amount of ground than hiking trails. The high biking activity in Kaupanger may affect red deer and more knowledge about the possible effects of mountain biking on red deer is therefore required.

Since deer often avoid roads and trails (Alves et al. 2014; Arnberger et al. 2008; Meisingset et al. 2013; Sibbald et al. 2011), I predicted deer occurrence to increase with increasing distance from the biking trails. Avoidance generally increases with the level of human activity (George & Crooks 2006; Meisingset et al. 2013; Sibbald et al. 2011); I, therefore, predicted deer occurrence to decrease with increasing trail width, a proxy for human activity. Furthermore, I predicted the effects of biking on red deer occurrence to be higher during the day, when human activity is high, compared with night. Finally, males and females often behave similarly relative to roads (Brown et al. 2012; Gagnon et al. 2007b; Laurian et al. 2008); I, therefore, predicted that females and males do not differ in their response to biking trails.

METHODS

Study area

This study was carried out in Kaupanger forest, Norway (61°11N, 7°14E). This area is located in boreonemoral zone. The pine-bilberry forest type is dominated by Scots pine, *Pinus sylvestris* (Moen 1999). I focused on pine-bilberry forest type with an age between 50-100 years. This forest type has good visibility, and consequently popular among bikers. The study area also comprise important feeding habitats for red deer (Mysterud et al. 2010). I used several biking trails around the village of Kaupanger (Fig. 1).

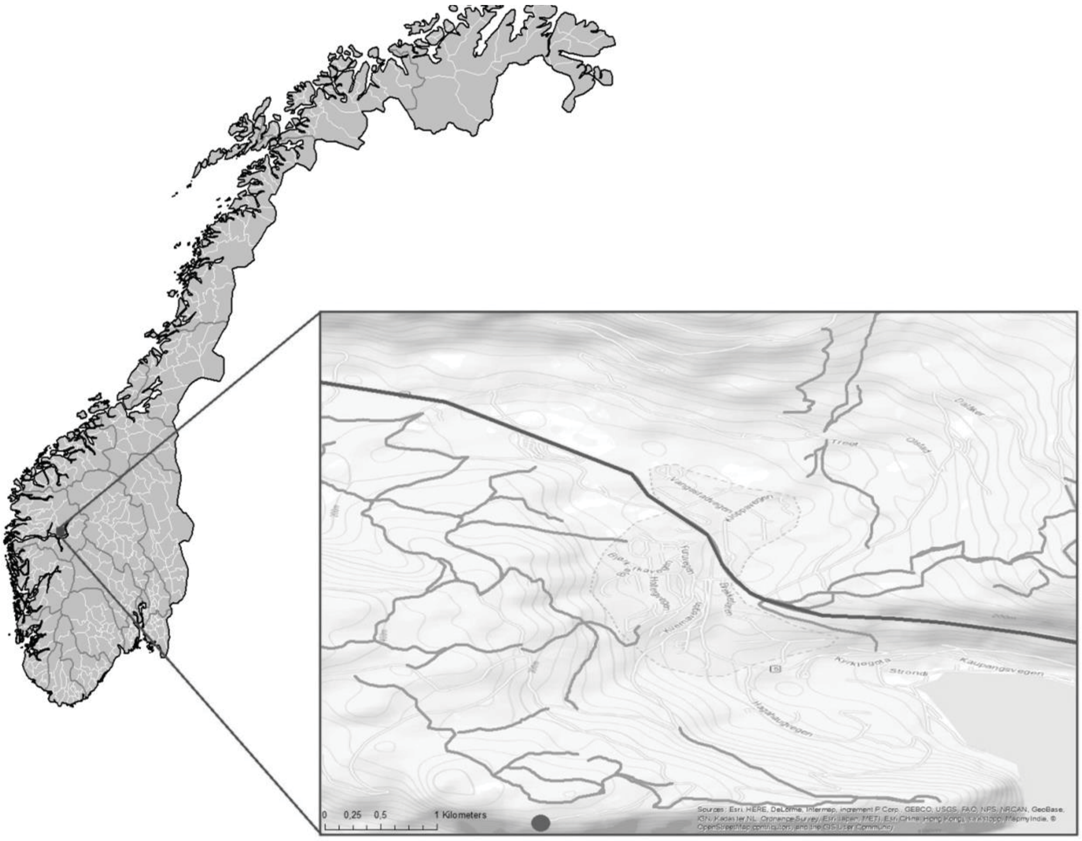

Fig. 1: The study area, where the main road (thick black line) is splitting the study area in two, with an area north (Hauståkermarki) and south (Holten) of the town Kaupanger. The grey thick lines show the distribution of biking trails and the dot in the south of the study area shows the supplementary feeding place.

The mean temperature is -2.9°C in winter (January) and 14.9°C in summer (July), with an annual precipitation of approximately 550 mm (YR 2015). The elevation varies between 200 and 500 m in the study area, although bikers also use the areas up to 1100 m.a.s.l. The main hiking trails are present in the same areas as the biking trails but in lower densities (Fig. 2).

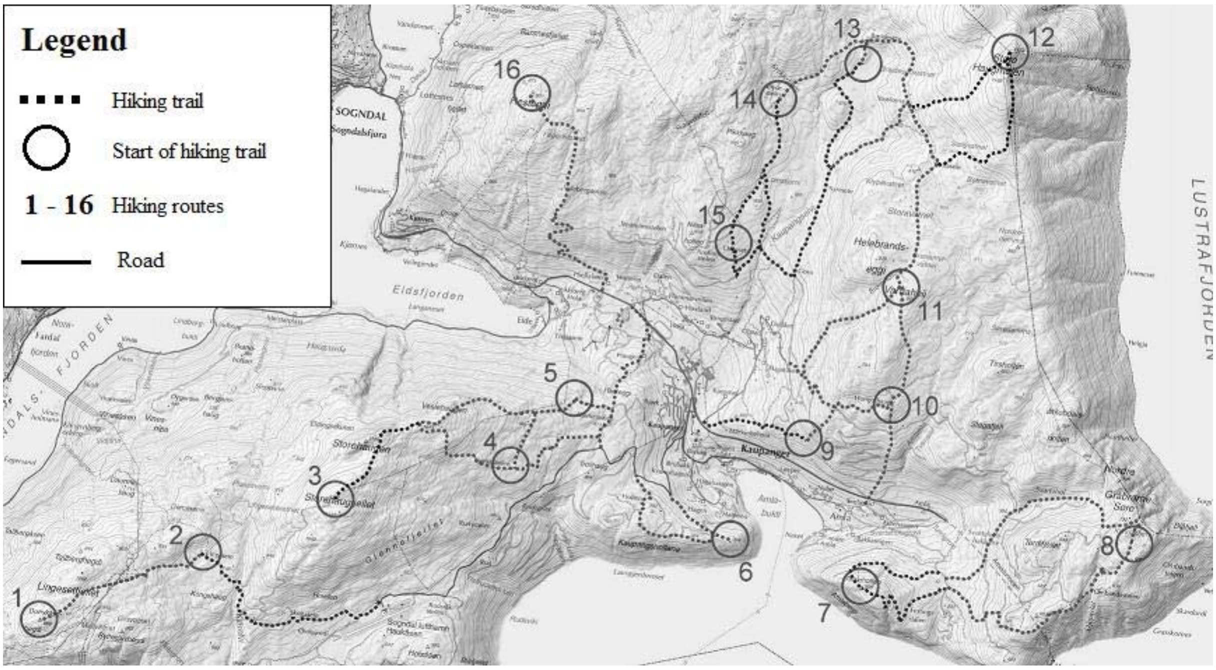

Fig. 2: The main hiking trails in and around the study area (Trimgruppa 2012).

Red deer is the dominating ungulate species in the study area, and the only ungulate species harvested. Roe deer (*Capreolus capreolus*) and moose (*Alces alces*) are currently not present as stable populations, while lynx (*Lynx lynx*) occurs at low densities and foxes *(Vulpus vulpus)* are relatively common (S.J. Hegland, Sogn og Fjordane University College, personal communication, March 13, 2015).

Data collection

Fieldwork was carried out between May and December 2015, using pellet group counts and camera traps. I counted pellet groups in randomly selected transects. All the transects were perpendicular to a biking trail, that was a straight line for at least two meter, throughout the study area (Appendix). Each transect consisted of 5x5m plots located 25 m apart (Fig. 3). Each plot was visited twice, spring (May) and autumn (October) 2015. The global position system (GPS) location of each plot was recorded on the first visit, allowing re-location on the second visit. I defined a pellet group as minimum 6 pellets (Acevedo et al. 2010) with maximum distance of 10 cm between them. I counted pellet groups by walking parallel lines from one end to the other end of a plot (Fig. 4). Pellets on the border of the plot were only recorded when at least half of the pellets were inside of the plot (Prokešová et al. 2006). For each season, I counted a total of 113 plots in 26 different transects.

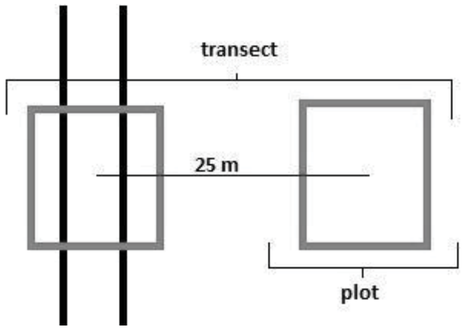

Fig. 3: Schematic representation of pellet group counting in plots (5x5m) that were 25m apart. The parallel black lines show the biking trail.

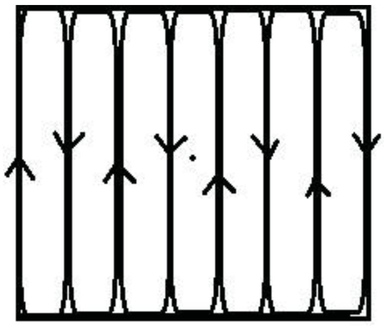

Fig. 4: Walking pattern for pellet group count in a plot, the arrows shows the walking direction.

I used remotely triggered cameras (Wingcam II TL) to record date and animal specific information on deer occurrence in relation to biking trails. Camera traps can assess the abundance and habitat use of animal species (Bowkett et al. 2007; Gregersen & Gregersen 2014; Kuijper et al. 2009). Furthermore, they give more information about diurnal activity and gender differences (Brown et al. 2012). I placed twelve camera traps, each at varying distances from biking trails (Appendix). The location of the cameras was determined by first randomly selecting a point on a biking trail. From this point, I walked perpendicular from the biking trail into the forest until I approached a deer track approximately parallel to the biking trail. I placed the camera traps on deer tracks to increase the probability of detection. If the approached deer track was at a distance (GPS-measured) closer than five meter of a distance already used within the area, I walked further until reaching the next deer track. When another biking trail was closer to the deer track than the starting point, I randomly selected another starting point. All cameras were placed within pine-bilberry forest at a height of 60-80 cm above ground. Cameras were set to take a series of three pictures per movement. The pictures were coloured during the day and black and white during the night using IR flash. The Central European Time (CET=UTC+1) was used for all cameras. Data collection began in May and ended in December 2015. I collected and checked the cameras in October and re-placed them, based on GPS locations, at the same location two or three days later. In December, all the cameras were collected. A camera remained at a site for an average of 161.25 nights (range: 53–189 nights). In total, there were 134 pictures recorded deer visits across 50 days.

Both roads and hiking trails often influence ungulate behaviour (Alves et al. 2014; Arnberger et al. 2008; Laurian et al. 2008; Sibbald et al. 2011); therefore transects and camera traps were always closer to a biking trail than a road or main hiking trail (based on Fig. 2) to minimize the influence of these factors. Furthermore, one supplementary feeding station, that might attract deer, was present in the study area (Fig. 1). I did not count pellets or placed cameras within 200 m of the feeding station.

Environmental variables

For each sampling plot and camera site, I noted the distance to the nearest biking trail (in m), the area where the plot or site was located, Hauståkermarki or Holten (Fig. 1), measured the basal area in m^2/ha (relascope sum) (Järvis 2013) and extracted the elevation (in m) from the GPS data. I used information about area, basal area and elevation to account for possible variations within these variables between plots or sites. Furthermore, with the pellet group count, I noted whether the biking trail was originally a deer trail or a tractor trail. All the trails used for the camera trap method were originally deer tracks. A biking trail that was originally a deer track will become wider with increasing use by mountain bikers; I, therefore, measured the width (in cm) of a biking trail as a proxy for human activity. The biking trails that were originally a tractor trail were already wide before bikers started using them; I, therefore, did not use the width of these old tractor trails. I obtained data on sunrise and sunset from www.timeanddate.no.

Statistical analyses

I used Generalized Linear Mixed Models (GLMM) with “poisson” distribution on the pellet group count data, using the function “glmer” from the R package “lme4” (Bates et al. 2015) to test the prediction that deer occurrence increase with increasing distance from the biking trails. I selected the most parsimonious model by using backward elimination from a full model (Crawley 2007). In the full model, number of pellet groups was the response variable and distance to trail, area, trail width, basal area, and elevation were fixed effects. To avoid pseudo-replication, I added transect number as a random factor. The least significant variables were eliminated until only statistically significant terms (P<0.05) were left in the model. Preliminary analysis revealed an apparent non-linear relationship between the response and distance. I, therefore, modelled the effect of distance using non-linear cubic splines (“ns” function in the R package “spline” (Venables & Ripley 2002)), with the optimal number of connection points (also called “knots”, where segments, defined by polynomial functions, come together and form a smoothing curve (Zuur et al. 2009)), determined through a comparison of AIC values calculated for models with different connection points (1-5). The model was fitted with the function “allEffects” from the R package “effects” (Fox 2003) and a prediction graph was made with the function “ggplot” from the R package “ggplot2” (Wickham 2009). In the autumn, the number of plots that had pellets was low (17 out of 113). Furthermore, sheep were present in some parts of the study area in the summer and due to similar size and shape, I could not distinguish deer from sheep pellets. For this reason and the low number of pellet groups found in the autumn, I only used data from spring in the statistical analyses.

I estimated the number of deer pictures, hereafter called visits, for each camera. I used binomial GLMM to test the predictions, that deer occurrence decreases with increasing trail width (human activity) and that the effect of biking on deer will be stronger during the day. To account for the difference in days a camera trap was active, I used the ratio between days with visits and days the camera was active as the response variable. Distance to biking trail, whether a picture was taken at night, between sunset and sunrise, or during the day, trail width, elevation, basal area and area were fixed effects. I added an interaction between distance and time (night/day) and trail width and time to test for a difference in effect of biking between day and night. I selected the most parsimonious model by using backward elimination from a full model. To avoid pseudo-replication, I added camera number as a random factor.

I tested the prediction that females and males do not differ in their response to biking trails with binomial GLMM using an aggregated dataset consisting only pictures where gender was identified. I used the ratio between days with visits and days the camera was active as response variable and distance to a biking trail, trail width and gender as fixed effects. I added an interaction between distance and gender and between trail width and gender to the model to check the prediction. I selected the most parsimonious model by using backward elimination from a full model. To avoid pseudo-replication, I added camera number as a random factor. Both models were fitted with the function “fit” from the R package “MuMIn” (Bartoń 2016) and prediction graphs were made with the function “ggplot” from R package “ggplot2” (Wickham 2009). All statistical analyses were performed in R version 3.1.2 for Windows.

Based on pellet group counting, I made an effect zone around the biking trails in ArcMap to visualise the extent to which red deer avoid biking trails. This map helps to visualise the size of the effect zone and shows the amount of disturbed habitat for red deer that is present in the study area.

RESULTS

In the spring, 76% of the plots (86 of the 113) contained red deer faecal pellet groups. Hauståkermarki contained more pellet groups than Holten and the number of pellet groups increased with increasing distance to biking trail (Table 1). The lowest number of pellet groups was found close to trails. This number increased up to about 40 m, followed by a slow decrease (Fig. 5).

Table 1: The effect of distance to a biking trail (m) and area (Hauståkermarki /Holten) on red deer occurrence (number of spring pellet groups) in Kaupanger, Norway. The numbers one to three are the individual connection points, where number two is most important. Other variables (basal area, trail width and elevation) had no significant effect (GLMM).

	Estimate β	SE	*z*	*P*-value
Intercept	0.253	0.250	1.013	0.311
ns (Distance, 3)1	0.282	0.280	1.007	0.314
ns (Distance, 3)2	2.190	0.437	5.015	< 0.001
ns (Distance, 3)3	0.092	0.411	0.223	0.823
Holten (vs. Hauståkermarki)	-0.571	0.230	-2.476	0.013

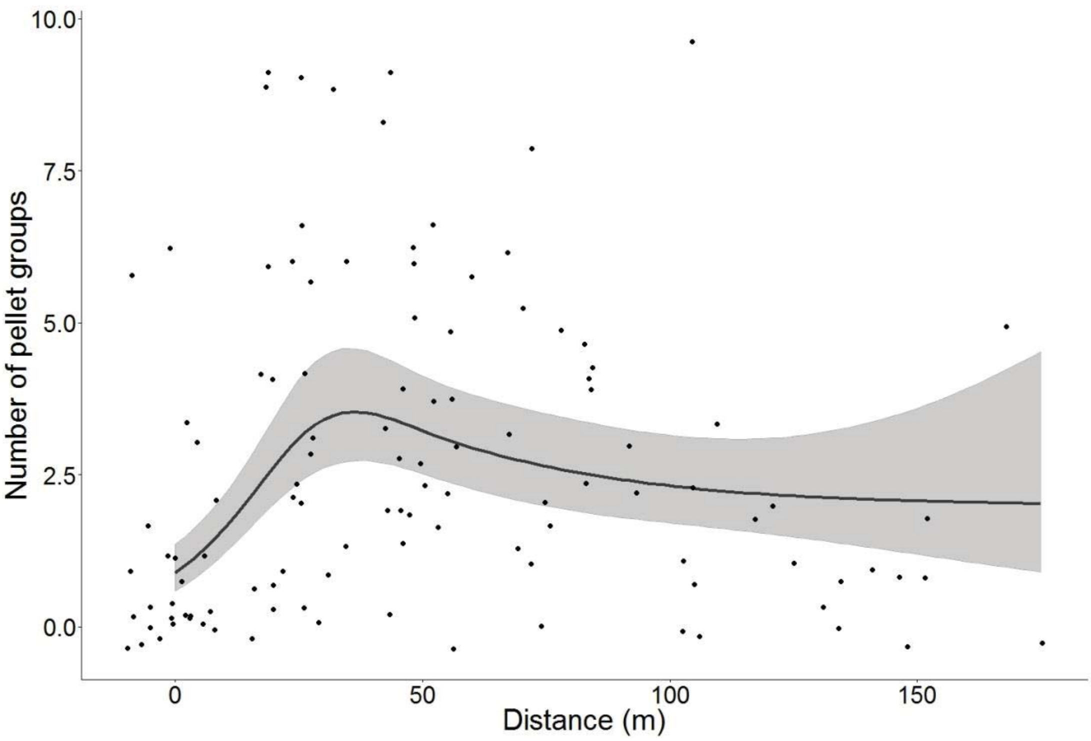

Fig. 5: The relationship between the number of pellet groups in the spring and the distance to a biking trail. The black line shows the prediction line and the grey area represent the 95% confident intervals.

Data from camera traps showed that trail width had a tendency to decrease the proportion of days with deer visit during the day compared to at night (Table 2). There were almost no deer visits during the day with a trail width larger than 50 cm (Fig. 6).

Table 2: The effect of trail width (cm) and time (night/day) on proportion of days with deer visits in Kaupanger, Norway. Other variables (basal area, elevation, distance and area) had no significant effect (GLMM).

	Estimate β	SE	*z*	*P*-value
Intercept	-3.583	0.335	-10.700	<0.001
Width	-0.005	0.005	-1.423	0.155
Day (vs. Night)	0.083	0.921	0.091	0.928
Width ~ Day (vs. Night)	-0.035	0.022	-1.603	0.109

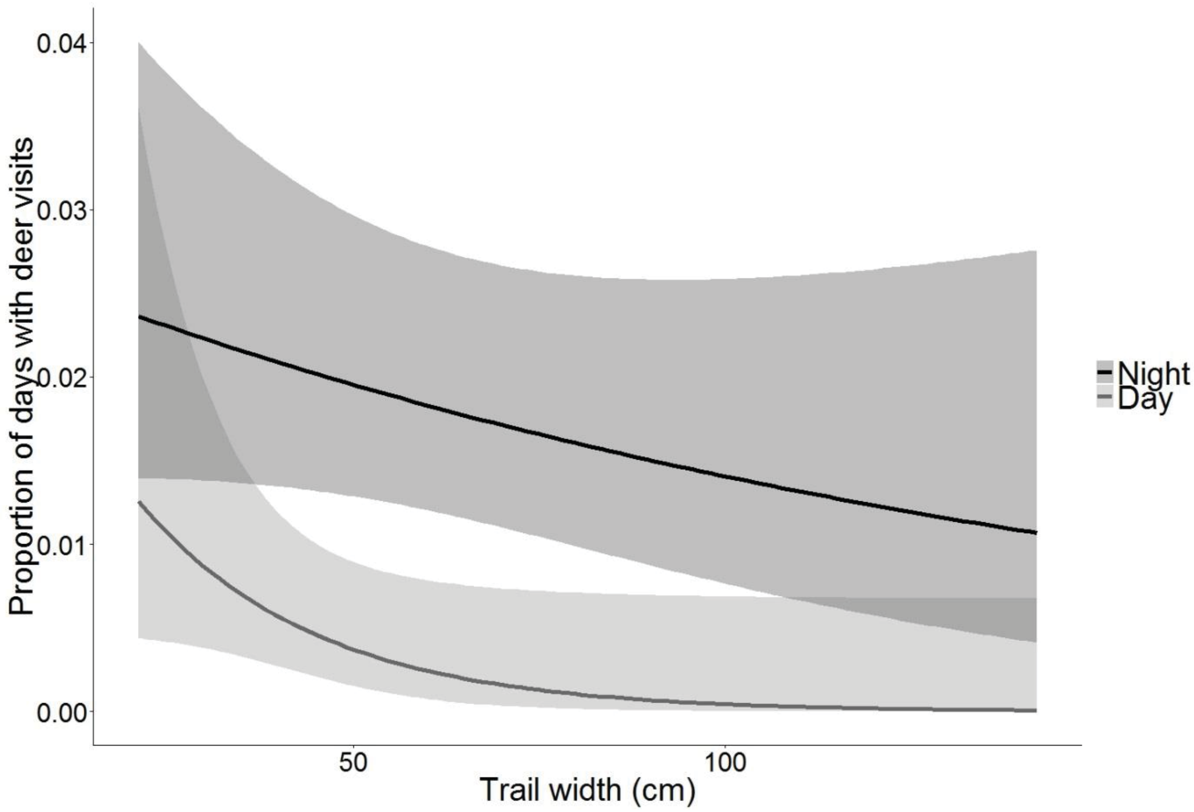

Fig. 6: The relationship between trail width and the proportion of days with deer visits. The black line shows the prediction line at night and the grey line shows the prediction during the day. The grey zones represent the 95% confident intervals.

An increase of trail width had a significant larger effect on males then on females (Table 3). The proportion of days a male deer visited decreased with increasing trail width, while there was no difference in proportion of days a female deer visited (Fig. 7).

Table 3: The effect of trail width (cm) on proportion of days with visits by male and female in Kaupanger, Norway. Other variables (basal area, distance, elevation and area) had no significant effect (GLMM).

	Estimate β	SE	*z*	*P*-value
Intercept	-4.596	0.526	-8.742	<0.001
Width	0.0001	0.007	0.019	0.985
Male (vs. Female)	2.038	1.014	2.011	0.044
Width ~ Male (vs. Female)	-0.063	0.025	-2.471	0.013

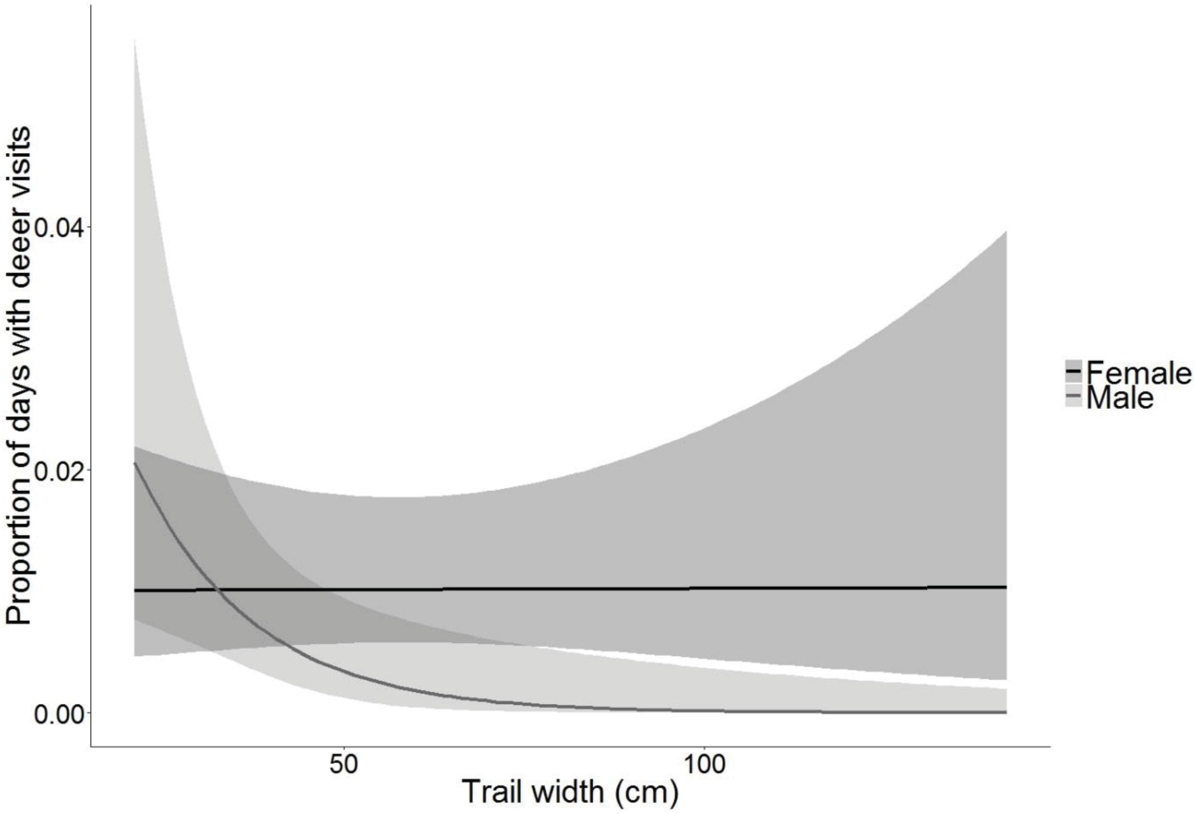

Fig. 7: The relationship between trail width and the proportion of days with deer visits. The black line shows the prediction line for females and the grey line shows the prediction for males. The grey zones represent the 95% confident intervals.

A zone of influence of 40 m, based on the pellet group counting, shows the areal extent of the disturbance of the biking trails (Fig. 8).

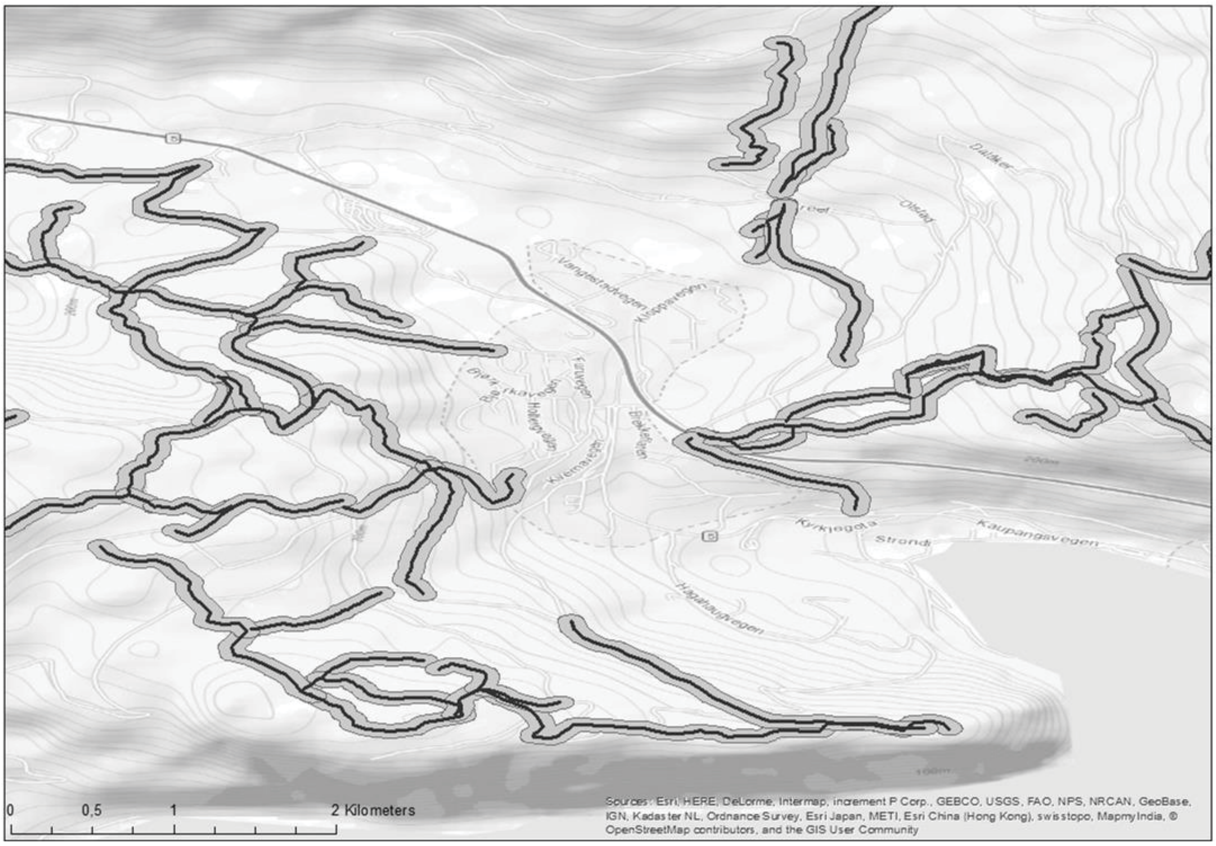

Fig. 8: Zone of influence of 40 m of the biking trails on red deer in Kaupanger, Norway.

DISCUSSION

The pellet group counts indicate that deer avoided biking trails up to 40 m. This result supports the prediction that deer occurrence will increase with increasing distance from the biking trails. Previous studies found that other species like bison, mule deer, pronghorn antelope (*Antilocapra americana*) and capercaillie (*Tetrao urogallus*), also avoid biking trails (Taylor & Knight 2003; Thiel et al. 2007). Avoidance of recreational trails can extend up to 400 m when the human activity is high (Rogala et al. 2011; Sibbald et al. 2011), although Licoppe and De Crombrugghe (2003) reported an avoidance of roads and tracks of 100 m by red deer. My results showed even a shorter avoidance distance than 100 m. However, I only considered biking trails and previous studies have shown that roads often have a stronger impact on ungulates (Alves et al. 2014; Bonnot et al. 2012; Dussault et al. 2007; Meisingset et al. 2013; Papouchis et al. 2001).

I predicted deer occurrence to decrease with increasing human activity (trail width), as found in other studies (George & Crooks 2006; Sibbald et al. 2011). I did not find a significant effect of human activity alone, but did find a tendency that deer occurrence decreased with increasing human activity during the day. This result, also partly supports my prediction that the effect of biking on deer occurrence would be higher during the day compared to night. Some studies found increasing avoidance by ungulates of a road or trail during the day compared to night (Godvik et al. 2009; Meisingset et al. 2013), whereas I did not found an interaction between distance to a biking trail and time (day/night).

The results did not support my prediction that females and males would not differ in their response to biking trails (Gagnon et al. 2007b; Laurian et al. 2008). Instead, I found that males were more responsive to human activity on biking trails than females. Males are often more vigilant to traffic then females (St. Clair & Forrest 2009; Taylor & Knight 2003) and an increase in human activity may therefore affect males more than females. However, females with calves can be more vigilant and show more flight behaviours than adults alone (Brown et al. 2012). Unfortunately, due to a low number of visits of young (n= 4 days), I could not separate female with young from female alone. Furthermore, gender identification was not possible for 19 deer visits, because the animal’s head was not shown. Trail width ranged from 21 cm to 142 cm. All the visits of male and 60% (14 out of 21 days) of female deer were from biking trails that were 54 cm or smaller. Only four out of twelve camera sites were located close to trail widths larger than 54 cm, of which three had trail width larger than 100 cm. While, there was no clear effect of trail width on females, more data on the effect of trail widths between 50 and 100 cm is required to show if human activity (measured as trail width) affect female deer.

Based on pellet group data, I found that deer avoided biking trails. Pellet group counting is regarded as an appropriate method to estimate distribution of deer (Acevedo et al. 2008; Alves et al. 2014; Smart et al. 2004). Deer defecate more when they are most active and when they stand up after resting (Collins & Urness 1981), whereas ungulates crossing roads have a higher movement rate (Dussault et al. 2007; Gagnon et al. 2007b; Leblond et al. 2011; Meisingset et al. 2013; Neumann et al. 2013) and have thus less time to defecate. However, before crossing a road, ungulates decide whether and where they will cross (Panzacchi et al. 2013). I found that further than 40 meter from a biking trail, deer occurrence slowly decreased. Deer may make a decicion to cross a biking trail at a distance around 40 meter, and thus stay longer in a place compared to further away from the biking trail, where deer experience no effect of a biking trail. Thus, the small decrease in number of pellet groups after 40 m distance of a biking trail may be due to deer returning to their normal behaviour.

I only found an effect of distance in the pellet group count data, whereas the effect of human activity was only appearant with the camera trap data. Pellet group counting is an effective method to calculate distribution of deer (Acevedo et al. 2008; Alves et al. 2014; Smart et al. 2004) and does not requires any expensive equipment. Camera traps are costly; however, placing them is less time consuming and they give more information about diurnal activity and gender differences (Brown et al. 2012). In this study, only two out of twelve camera traps were closer than 40 m to a biking trail. Any short distance effect, as found with pellet group counting, may therefore difficult to detect. I did find a stronger avoidance behaviour with increasing human acitivity during the day compared to during the night and in males compared to females, a trend that could not be detected with pellet group counting. However, trail width alone was not significant and was therefore not detected with the pellet group data. An increase in human activity may increase the zone of influence of a species (Cameron et al. 2004; George & Crooks 2006; Rogala et al. 2011); therefore the avoidance found in this study could be larger than 40 m during the day and/or in males.

In Kaupanger, most deer follow the regular migration pattern for Norwegian red deer: they inhabit pine-bilberry forest area in autumn and migrate to a higher altitude summer habitat in the spring (Bischof et al. 2012; Meisingset et al. 2013). I assumed that the pellets I counted in the spring were aggregated in the winter and spring and the pellets I counted in the autumn where aggregated in the summer and the autumn, when the deer density is low. The low deer density, in addition to higher decomposition rate in summer, explains the low number of pellet groups I found in the autumn (26) compared to the spring (302). Due to this low number in pellet groups and since it may be hard to distinguished sheep and deer pellets in the autumn, I did not use the pellet group counts done in this season. Therefore, the result that deer avoid areas 40 m from a biking trail is only based on deer behaviour in winter and spring.

Some studies based on disturbance by human activity found a much larger zone of influence than found in this study (Cassirer et al. 1992; Rogala et al. 2011; Sibbald et al. 2011). Ungulates may habituate to a disturbance if they do not experience it as a threat (Papouchis et al. 2001; Recarte et al. 1998; Stankowich 2008). It could be that red deer habituated to mountain biking in Kaupanger and gradually reduced their avoidance of biking trails. However, hunting also affects an animal’s behaviour (Marchand et al. 2014; Sunde et al. 2009; Thurfjell et al. 2013) and may even reduce habituation (Kloppers et al. 2005). In Norway, the hunting period is from September to December and the hunting area for red deer in Kaupanger covers nearly the total area available for mountain biking. In 2014, 509 red deer were harvested in the municipality of Sogndal, from which around 52% were harvested in Kaupanger (Hjorteviltregisteret 2014). Due to the hunting, deer may be more alert and are, therefore less likely to habituate to the biking.

In the winter, there is some skiing and biking on snow, mostly off-trail (S.J. Hegland, Sogn og Fjordane University College, personal communication, March 15, 2016). Off-trail recreation is unpredictable and thus often have a larger effect on wildlife then on-trail (Bateman & Fleming 2014; Miller et al. 2001; Stankowich 2008; Taylor & Knight 2003; Wolf & Croft 2010). I only studied the effect of on-trail biking on red deer, whereas off-trail biking may affect red deer differently. Experiments with approaching deer give more information about the effect of off-trail recreation (Langbein & Putman 1992; Miller et al. 2001). Furthermore, this method allows one to study different behaviours (vigilant, flight, traveling and defensive) towards bikers or other recreationist. It would be interesting to see how red deer react to bikers and if off-trail biking affect deer different then on-trail.

Ungulates often adjust their habitat use to avoid roads or trails (Jayakody et al. 2008; Longshore et al. 2013; Manor & Saltz 2005; Rogala et al. 2011). The combination of pellet group counts and camera traps is an efficient way of recording area use of deer (Acevedo et al. 2008; Alves et al. 2014; Brown et al. 2012; Smart et al. 2004) . However, the data is best for small-scale studies. For studies on a larger scale one needs to intensify sampling regimes or include data from GPS-collared deer (Beauchesne et al. 2014; Laurian et al. 2008; Marchand et al. 2014; Mysterud et al. 2010; Rogala et al. 2011). Unfortunately, GPS collars are expensive and beyond the resources of this project. In this study, I found an average avoidance distance based on the pellet group data, but ungulates fluctuate in there avoidance of roads or trails (Cassirer et al. 1992; Gagnon et al. 2007b; Longshore et al. 2013; Meisingset et al. 2013; Sibbald et al. 2011). GPS data could also give better and more detailed results about these possible fluctuations in avoidance distance.

An increase in biking activity may, not only cause an increase in trail avoidance by deer, that decreases the size of undisturbed areas, but also result in more biking trails, that will cut the undisturbed areas in several even smaller areas. In this study, I found that deer avoided biking trails up to 40 m and with increasing biking activity not only this zone of influence may increase but it may also decrease the amount of area where the deer do not experience any disturbance. In addition to biking trails, also hiking trails and roads are present in the area. Some studies have found that humans on foot are causing even larger disturbance than mountain bikers or other vehicles (Brown et al. 2012; Papouchis et al. 2001; Stankowich 2008), however others found no or a small difference between biking and hiking (George & Crooks 2006; Naylor et al. 2009; Taylor & Knight 2003). From the highway, that splits the study area in two (Fig 1), several smaller roads are transecting the area. The effect of roads on red deer seems to be small (0-100m) (Alves et al. 2014; Meisingset et al. 2013), however a large number of roads and trails may decrease the amount of suitable habitat causing animals to adjust the home ranges (Beauchesne et al. 2014; Laurian et al. 2008). It would be interesting to investigate how these multiple disturbance factors affect red deer.

In conclusion, this study shows that red deer in Kaupanger, Norway, avoid biking trails. While I found no difference in deer occurrence in relation to distance to a biking trail between day and night, I did find a tendency that deer occurrence decreased with increasing human activity during the day. Furthermore, males reacted stronger to an increase of human activity than females. An increase of biking activity in the area often lead to more trails and an increase in avoidance of deer toward wider trails and, thus eventually to less suitable deer habitat.

REFERENCES

Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A. R., Alzaga, V. & Gortázar, C. (2008). Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology*, 276: 37-47.

Acevedo, P., Ferreres, J., Jaroso, R., Durán, M., Escudero, M. A., Marco, J. & Gortázar, C. (2010). Estimating roe deer abundance from pellet group counts in Spain: An assessment of methods suitable for Mediterranean woodlands. *Ecological Indicators*, 10: 1226-1230.

Alves, J., Alves da Silva, A., Soares, A. M. V. M. & Fonseca, C. (2014). Spatial and temporal habitat use and selection by red deer: The use of direct and indirect methods. *Mammalian Biology*, 79: 338-348.

Arnberger, A., Eder, R., Frey-Roos, F., Nopp-Mayr, U., Tomek, H., Muralt, G. & Zohmann, M. (2008). *The management challenge between urban recreation demands and nature conservation*. 4th Symposium of the Hohe Tauern National Park for research in protected areas, Castle of Kaprun, pp. 17-19.

Bartoń, K. (2016). *MuMIn: Multi-Model Inference*.

Bateman, P. W. & Fleming, P. A. (2014). Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *Journal of Zoology*, 294: 93-98.

Bates, D., Machler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67: 1-48.

Beauchesne, D., Jaeger, J. A. G. & St-Laurent, M.-H. (2014). Thresholds in the capacity of boreal caribou to cope with cumulative disturbances: Evidence from space use patterns. *Biological Conservation*, 172: 190-199.

Belotti, E., Heurich, M., Kreisinger, J., Šustr, P. & Bufka, L. (2012). Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements. *Animal Biodiversiy and Conservation*, 35: 235–246.

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B. & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *The American Naturalist*, 180: 407-24.

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F. & Hewison, A. J. M. (2012). Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research*, 59: 185-193.

Borkowski, J. J., White, P. J., Garrott, R. A., Davis, T., Hardy, A. R. & Reinhart, D. J. (2006). Behavioral responses of bison and elk in yellowstone to snowmobiles and snow coaches. *Ecological Applications*, 16: 1911–1925.

Bowkett, A. E., Rovero, F. & Marshall, A. R. (2007). The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *African Journal of Ecology*, 46: 479–487.

Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R. & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. *PLoS One*, 7: e40505.

Cameron, R. D., Smith, W. T., White, R. G. & Griffith, B. (2004). Central arctic caribou and petroleum development: Distributional, nutritional, and reproductive implications. *Artic*, 58: 1-9.

Cassirer, F. E., Freddy, D. J. & Ables, E. D. (1992). Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin*, 20: 375-381.

Collins, W. B. & Urness, P. J. (1981). Habitat preferences of mule deer as rated by pellet-group distributions. *The Journal of Wildlife Management*, 45: 969-972.

Colman, J. E., Lilleeng, M. S., Tsegaye, D., Vigeland, M. D. & Reimers, E. (2012). Responses of wild reindeer (Rangifer tarandus tarandus) when provoked by a snow-kiter or skier: A model approach. *Applied Animal Behaviour Science*, 142: 82-89.

Crawley, M. J. (2007). *The R book*. Imperial College London at Silwood Park, UK: John Wiley & Sons Ltd.

Davis, C. A., Leslie, D. M., Walter, W. D. & Graber, A. E. (2010). Mountain biking trail use affects reproductive success of nesting golden-cheeked warblers. *The Wilson Journal of Ornithology*, 122: 465-474.

Dussault, C., Ouellet, J.-P., Laurian, C., Courtois, R., Poulin, M. & Breton, L. (2007). Moose movement rates along highways and crossing probability models. *Journal of Wildlife Management*, 71: 2338-2345.

Frid, A. & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Biology*, 6: 11.

Gagnon, J. W., Schweinsburg, R. E. & Dodd, N. L. (2007a). *Effects of roadway traffic on wild ungulates: A review of the literature and case study of elk in Arizona*. Proceedings of the 2007 International Conference on Ecology and Transportation. North Carolina State University: Center for Transportation and the Environment.

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Boe, S. & Schweinsburg, R. E. (2007b). Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management*, 71: 2318-2123.

George, S. L. & Crooks, K. R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, 133: 107-117.

Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009). Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, 90: 699–710.

Gregersen, H. & Gregersen, F. (2014). Wildlife cameras effectively survey black grouse Lyrurus tetrix leks. *Ornis Norvegica*, 37: 1−6.

Guillemain, M., Blanc, R., Lucas, C. & Lepley, M. (2007). Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. *Biodiversity and Conservation*, 16: 3633-3651.

Hegland, S. J. (2012). Høgrisikostrekningar for hjortepåkøyrsler langs riksvegnettet i Sogn og Fjordane: Rangering, tiltak og prioritering. *Fagrapport 2/11*. Svanøy/Sogndal: Norsk Hjortesenter. 1-33 pp.

Hjorteviltregisteret. (2014). *Felte hjort i prosent*. Available at: http://www.hjorteviltregisteret.no/Hjort/Jaktstatistikk/FelteDyrStatistikk (accessed: 29-04-2015).

Järvis, J. (2013). Forest measurement with relascope. Practical description for fieldwork with examples for Estonia.

Jayakody, S., Sibbald, A. M., Gorson, I. J. & Lambin, X. (2008). Red deer viligance behaviour differs with habitat and type of human disturbance. *Wildlife Biology*, 14: 81-91.

Jiang, G., Zhang, M. & Ma, J. (2007). Effects of human disturbance on movement, foraging and bed selection in red deer. *Acta Theriologica*, 52: 435–446.

Kloppers, E. L., St. Clair, C. C. & Hurd, T. E. (2005). Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society*, 10: 31.

Kuijper, D. P. J., Cromsigt, J. P. G. M., Churski, M., Adam, B., Jędrzejewska, B. & Jędrzejewski, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management*, 258: 1528-1535.

Langbein, J. & Putman, R. J. (1992). Behavioural responses of park red and fallow deer to disturbance and effects on population performance. *Animal Welfare*, 1: 19-38.

Lathrop, J. (2003). *Ecological impacts of mountain biking: A critical literature review*: WildEarth Guardian. Available at: http://www.wildlandscpr.org/ecological-impacts-mountain-biking-critical-literature-review (accessed: 20-1-2015).

Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M. & Breton, L. (2008). Behavior of moose relative to a road network. *Journal of Wildlife Management*, 72: 1550-1557.

Leblond, M., Frair, J., Fortin, D., Dussault, C., Ouellet, J.-P. & Courtois, R. (2011). Assessing the influence of resource covariates at multiple spatial scales: An application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecology*, 26: 1433-1446.

Licoppe, A. M. & De Crombrugghe, S. A. (2003). Assessment of spring habitat selection of red deer (Cervus elaphus L.) based on census data. *Zeitschrift Fur Jagdwissenschaft* 49: 1-12.

Longshore, K., Lowrey, C. & Thompson, D. B. (2013). Detecting short-term responses to weekend recreation activity: Desert bighorn sheep avoidance of hiking trails. *Wildlife Society Bulletin*, 37: 698-706.

Manor, R. & Saltz, D. (2005). Effects of human disturbance on use of space and flight distance of mountain gazelles. *Journal of Wildlife Management*, 69: 1683-1690.

Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D. & Loison, A. (2014). Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biological Conservation*, 177: 1-11.

Marion, J. & Wimpey, J. (2007). Environmental impacts of mountain biking: Science review and best practices. In Webber, P. (ed.) *Managing Mountain Biking: IMBA's Guide to Providing Great Riding*, pp. 94-111. Boulder: International Mountain Bicycling Association (IMBA).

Meisingset, E. L., Loe, L. E., Brekkum, Ø., Van Moorter, B. & Mysterud, A. (2013). Red deer habitat selection and movements in relation to roads. *The Journal of Wildlife Management*, 77: 181-191.

Miller, S. G., Knight, R. L. & Miller, C. K. (2001). Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin*, 29: 124-132.

Moen, A. (1999). *National atlas of Norway vegetation*. Hønefoss: Norwegian mapping authority.

Mysterud, A., Askilsrud, H., Loe, L. E. & Veiberg, V. (2010). Spatial patterns of accumulated browsing and its relevance for management of red deer Cervus elaphus. *Wildlife Biology*, 16: 162-172.

Naylor, L. M., J. Wisdom, M. & G. Anthony, R. (2009). Behavioral responses of North American elk to recreational activity. *Journal of Wildlife Management*, 73: 328-338.

Neumann, W., Ericsson, G. & Dettki, H. (2009). Does off-trail backcountry skiing disturb moose? *European Journal of Wildlife Research*, 56: 513-518.

Neumann, W., Ericsson, G., Dettki, H. & Radeloff, V. C. (2013). Behavioural response to infrastructure of wildlife adapted to natural disturbances. *Landscape and Urban Planning*, 114: 9-27.

Panzacchi, M., van Moorter, B. & Strand, O. (2013). A road in the middle of one of the last wild reindeer migration routes in Norway: Crossing behaviour and threats to conservation. *Rangifer*, Special Issue: 15-26.

Papouchis, C. M., Singer, F. J. & Soal, W. B. (2001). Responses of desert bighorn sheep to increased human recreation. *The Journal of Wildlife Management*, 65: 573-582.

Prokešová, J., Barančeková, M. & Homolka, M. (2006). Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest. *Folia Zoologica*, 55: 1-14.

Quinn, M. & Chernoff, G. (2010). Mountain Biking: A review of the ecological effects. A literature review for parks Canada – National Office (Visitor Experience Branch). Calgary: Miistakis institute. 1-40 pp.

Recarte, J. M., Vincent, J. P. & Hewison, A. J. M. (1998). Flight responses of park fallow deer to the human observer. *Behavioural Processes*, 44: 65–72.

Reimers, E. & Colman, J. E. (2006). Reindeer and caribou (Rangifer tarandus) response towards human activities. *Rangifer*, 26: 55-71.

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A. & Coleshill, J. (2011). Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecology and Society*, 16: 16.

Seip, D. R., Johnson, C. J. & Watts, G. S. (2007). Displacement of mountain caribou from winter abitat by snowmobiles. *Journal of Wildlife Management*, 71: 1539-1544.

Sibbald, A. M., Hooper, R. J., McLeod, J. E. & Gordon, I. J. (2011). Responses of red deer (Cervus elaphus) to regular disturbance by hill walkers. *European Journal of Wildlife Research*, 57: 817-825.

Skarin, A., Danell, Ö., Bergström, R. & Moen, J. (2010). Reindeer movement patterns in alpine summer ranges. *Polar Biology*, 33: 1263-1275.

Smart, J. C. R., Ward, A. I. & White, P. C. L. (2004). Monitoring woodland deer populations in the UK: An imprecise science. *Mammal Review*, 34: 99–114.

St. Clair, C. C. & Forrest, A. (2009). Impacts of vehicle traffic on the distribution and behaviour of rutting elk, Cervus elaphus. *Behaviour*, 146: 393-413.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, 141: 2159-2173.

Sunde, P., Olesen, C. R., Madsen, T. L. & Haugaard, L. (2009). Behavioural responses of GPS-collared female red deer Cervus elaphusto driven hunts. *Wildlife Biology*, 15: 454-460.

Taylor, A. R. & Knight, R. L. (2003). Wildlife responses to recreation and associated visitors perspection. *Ecological Applications*, 13: 951-963.

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R. & Jenni, L. (2007). Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: A new methodological approach. *Journal of Applied Ecology*, 45: 845-853.

Thurfjell, H., Spong, G. & Ericsson, G. (2013). Effects of hunting on wild boar Sus scrofa behaviour. *Wildlife Biology*, 19: 87-93.

Torres, R. T., Santos, J. & Fonseca, C. (2014). Factors influencing red deer occurrence at the southern edge of their range: A Mediterranean ecosystem. *Mammalian Biology*, 79: 52-57.

Trimgruppa, K. (2012). *Topptrimmen på Kaupanger*. Available at: http://www.kaupanger.no/files/2012/06/kart_til_flygeblad_2012.jpg.

Venables, W. N. & Ripley, B. D. (2002). *Modern applied statistics with S*, vol. Fourth edition. New York, USA: Springer Verlag.

Vistness, I. & Nellemann, C. (2001). Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management*, 65: 915-925.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*: Springer-Verlag New York.

Wisdom, M. J., Cimon, N. J., Johnson, B. K., Garton, E. O. & Thomas, J. W. (2004). *Spatial partitioning by mule deer and elk in relation to traffic*. Reprinted from the 2004 Transactions of the North American Wildlife and Natural Resources Conference ed. The Starkey Project: a synthesis of long-term studies of elk and mule deer. Kanses, USA: Alliance Communications Group, Lawrence. 53-66 pp.

Wolf, I. D. & Croft, D. B. (2010). Minimizing disturbance to wildlife by tourists approaching on foot or in a car: A study of kangaroos in the Australian rangelands. *Applied Animal Behaviour Science*, 126: 75-84.

YR. (2015). *Klimastatistikk for Vestlandet*. Available at: http://www.yr.no/sted/Norge/Sogn_og_Fjordane/L%C3%A6rdal/L%C3%A6rdals%C3%B8yri_m%C3%A5lestasjon/klima.html (accessed: 29-04-2015).

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Statistics for Biology and Health: Springer New York.

APPENDIX

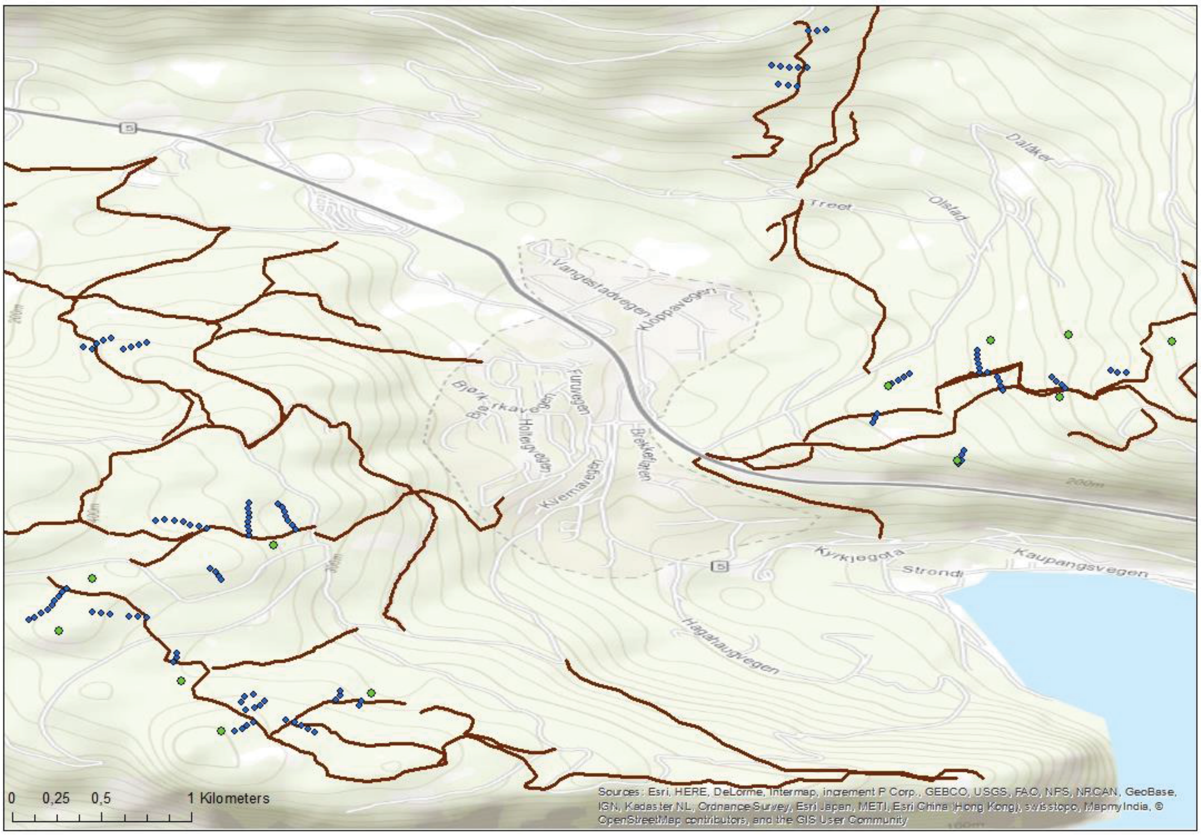

Fig I: The location of the camera traps (green dots), plots of the pellet group counts (blue dots) and the biking trails (brown line) within the study area.

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no