TO RUN OR STAY - ANTI-HUNTER BEHAVIOUR OF FEMALE MOOSE

Steffen Johnsen

Master Thesis
at Faculty of Applied Ecology and Agricultural Sciences

HEDMARK UNIVERSITY COLLEGE

2013

Abstract

In Norway, hunting is the main mortality factor of moose (*Alces alces*), with hunters killing approximately ¼ of the fall population each year. During 2009 and 2010 I studied escape behaviour of GPS/VHF-marked female moose when disturbed by humans, using 2 different methods: 1) Observing the hourly movements of individual moose in June when calving status was checked and during the hunting season while stalked by my hunting team; 2) Comparing the daily movements of GPS–moose during the hunting season in hunting units with and without hunters. During calf checking, no female moose defended her calf by aggressive behaviour; instead, the cows moved off, covering a mean distance of 1364 m (min: 117 m, max: 7326 m) before settling down after 2 hours. This indicated that human activity in the forest during the calving season involved little risk for either calves or humans. When flushed during the hunting season, the cows moved a significantly longer distance (mean 2338 m, min: 111 m, max: 6879 m). There were large differences within and between individuals in how far they moved when flushed. Again, no individuals showed aggressive behaviour. Some consistently fled a short distance, some always a long distance, and some were inconsistent, but flight distance was unrelated to survival during the hunting season. The distances cows moved decreased during the hunting season, regardless of disturbance. When hunters were present in a hunting unit, the daily movements of moose cows within the unit increased by an average factor of 1.16 and the percentage of moose moving more than the expected upper daily travel distance increased from 10 to 16.5 %. Although most moose will be shot sooner or later, the probability of a moose being killed when observing a human was low. Some moose were able to sneak around the observer, but most fled a distance sufficient to move out of a hunting unit of mean size 13 km^2. I suggest that selection by human hunters against standing still and being aggressive may be a reason for the apparent naivety of moose towards recolonizing wolves (*Canis lupus*) in Scandinavia.

Steffen Johnsen

Evenstad, May

Steffen Johnsen

Introduction

Evolution selects the traits of individuals with the greatest fitness (Darwin, 1859). High fitness is obtained by high survival of adults and the production of competitive offspring (Darwin, 1859). In all prey species, production and survival depend on an individual's ability to obtain high quality forage and avoid predators (Franzmann and Schwartz, 2007). Moose (*Alces alces*) is the largest species in the deer family and inhabits the Northern Hemisphere (Odum, 1983; Telfer, 1984; Franzmann and Schwartz, 2007). In North America, wolves (*Canis lupus*) and bears (*Ursus arctos*) are the main predators of moose (Franzmann and Schwartz, 2007), but in Fennoscandia wolf and brown bear populations have been heavily depressed and controlled by man for several hundreds of years (Wabakken, 1986; Wabakken and Maartmann, 1994). This, together with changes in forest cutting regimes, decreasing use of forest pastures for grazing domestic livestock, and changing hunting regimes since the 1970s, has allowed the moose populations in Norway and Sweden to increase to the highest densities ever recorded (Lavsund, et.al., 2003). However, in recent decades restricted large carnivore populations have re-establish in parts of Sweden and in neighbouring Norwegian areas (Wartiainen, et.al., 2010; Wabakken, et al., 2012).

Due to low wild predator densities in Fennoscandia today, man is the main moose predator, each year harvesting about 25 % of the population (Solberg, et.al., 1999). During the last decade, annual moose harvests have been about 35 000 in Norway, 100 000 in Sweden and 58 000-75 000 in Finland (Statistics Norway, 2012; Svenska Jägareförbundet, 2012; Finnish Game and Fisheries Research Institute, 2012). However, within the few recovering Norwegian wolf territories, wolves predate moose, especially new born calves (Sand, et.al, 2005). Wolverines (*Gulo gulo*) can also kill moose, but only under very favourable snow conditions (Kozhechkin, et.al, 2005; Magoun, et.al, 2005). Gundersen (2003) showed that in a Norwegian wolf territory 8.1% of the moose population was killed by wolves.

Predation has a strong impact on the development of behavioural characteristics of prey species, for example anti-predator behaviour (Harvey and Greenwood, 1978; Sand, et.al., 2005), which varies temporarily and spatially in relation to predation risk (Sönnichsen et al. 2013). Avoidance of predation by human hunters is also likely to be a strong selecting force (Ciuti,et.al, 2012). Partly before, but always since the Norwegian Hunting law of 1899, moose cows and their calves have been protected during summer. I would therefore not expect any specific selection pressure for anti-human behaviour in summer, in line with the risk allocation hypothesis (Sönnichsen, et al., 2013).

There is a growing interest in understanding the effects of human disturbance, such as hunting, on our animal populations (Neumann, et.al, 2009; Ciuti,et.al, 2012). Moose and moose hunting have long traditions in Norway (Lykke, 2005). Previous studies of moose have shown that encounters with people can trigger anti-predator behaviour (Neumann, et.al, 2009), with the consequence that they spend more time scouting and less time foraging and on reproductive behaviour (Rolandsen, et al.,

2010). Moose are most likely to survive if they stand still and are aggressive against wolves (Peterson, 1977), since when they run, 90% of wolf attacks on moose occur within 400 m (Wikenros, et.al, 2009). However, when hunted by humans, it is essential for the moose to avoid being shot but also to minimise expenditure of time and energy running away. Moose therefore have to decide when to react. Earlier studies have shown that only 75% of the moose fled when observers approached to about 100 m from the moose (Root, et.al, 1988; Andersen, et.al, 1995). Thus moose react differently depending on the predator and have 3 different options: 1) stand still and be aggressive against the predator; 2) run far away from the predator, and 3) sneak around the predator, hoping not to be detected or attacked.

Few published studies have quantified the spatial aspects of escape behaviour of moose when confronted by hunters. Quantifying movements is important because we need to understand escape behaviour in order to understand and manage the interactions between human as predator and its prey (Baskin, et.al, 2004). Most of the published studies have looked at the differences between sex and group size. Fritz (2008) looked at how hunting activity effected the movement of moose comparing movements before and during the hunting season. In this study I looked at how GPS-marked moose responded when actively flushed by an observer in June and during the hunting season. I also studied how the movement patterns of GPS-collared moose inside hunting units changed during days of ordinary recreational hunting. I tried to assess how the predation pressure from hunters affected moose anti-predation behaviour.

Methods

Study area

The study area was located in Stor-Elvdal municipality (61°N, 11°E), Hedmark County in eastern Norway. The study area was 1370 km^2 of predominantly commercially managed boreal forest on either side of the river Glomma, Norway longest river (Milner, et.al, 2012). Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the dominant tree species, but birch (*Betula pubesens*), rowan (*Sorbus ancaparia*), aspen (*Populus tremula*), grey alder (*Alnus incana*), goat willow (*Salix caprea*) and willow (*Salix spp.*) were also presented. The moose hunting season was from 25th September to 23rd December and 733 moose were shot in Stor-Elvdal in the 2012 hunting season (Statistics Norway, 2012). Moose density varied during the year, with moose congregating in areas of less deep snow during winter. Wintering density was estimated to be approximately 1.3 moose per km^2 at the landscape scale (Milner, et.al., 2012).

Mature adult female moose were captured during winter as part of a wider study (see van Beest et al., 2012 and Milner et al., 2012). All moose were darted from a helicopter (see Arnemo, et.al., 2003 for details) and fitted with GPS-collars with VHF-transmitters (Tellus Remote GPS, Followit AB, Lindesberg, Sweden). The GPS-collars were programmed to take positions every hour and send them

by SMS when within GMS-range. For this study 32 GPS-marked female moose (13 in 2009 and 19 in 2010) were used. All females had successfully calved the previous year.

Field methods

In June I checked how many calves each marked female moose had (Milner et. al., 2012). Moose cows were approached on foot by radio-tracking using earphones, walking slowly, stalking into the wind and using good camouflage. In total 35 successful observations of 31 cows were made.

I sampled data in the hunting season by 2 methods. 1) Flight distances were recorded when directly disturbed during culling of specific, individually marked moose with our hunting team. The size of the team varied from 1 to 10 people. Although Norwegian moose hunting often involves the use of loose hounds, I excluded such hunts from our dataset because of the difficulty in getting the dog to follow one specific moose. In every culling attempt I noted the time at which the moose fled and how many hunters we were. Culling a specific individual turned out to be much harder than expected. The movements of 11 different marked female moose were investigated during culling.

2) Daily movements of marked moose were monitored during ordinary recreational hunting. In Norway all hunting teams must fill out a mandatory hunter observation form (SETT ELG: National Cervid Monitoring Program) of how many team members they have and what animals they see and shoot every day in their hunting unit. I compared the movements of marked moose on days with and without hunters in the hunting unit. 25 different marked female moose were used for this.

Data analyses

Flight distances when directly disturbed during calf checking and culling

I used the GPS-positions sampled from the GPS-collars to estimate the flight distance, as the distance moved from the moment the moose started running to the moment it settled down again, using Pythagorean Theorem. I regarded moose to have settled down when the distance moved per hour equalled their normal speed, estimated for each individual before hunters were in the terrain. I modelled the probability of survival during the hunting season in relation to log-transformed flight distance, corrected for date and season, using generalised mixed models (GLMM) with individual ID fitted as a random effect and assuming binomially-distributed errors.

Daily movements during recreational hunting

I plotted all the GPS positions from the hunting season for both years onto a map of the hunting units in the study area using a geographic information system (ArcGIS). SETT ELG gave information of the number of hunters within each hunting unit each day. For each moose, every day, I calculated the distance (m) moved. I used mixed linear models in R (R Development Core Team, 2009) and backward selection using AIC-values to determine whether number of hunters, number of calves, numbers of moose seen while hunting, wind speed, date, snow depth, rain, temperature and hunting influenced moose movements. All distances were log-transformed.

Expected distance moved

I calculated the 90th percentile of the daily distance moved from all days without hunters in the hunting unit. To find the expected hourly distance moved we divided the expected daily distance moved by 24. When the moose moved further than the distance estimate they were interpreted to have moved more than expected and thereby be disturbed.

Results

During calf checking and culling the adult female moose fled in 58 cases (88 %) and sneaked away in 8 cases (12 %) while in 0 cases did they stand still and be aggressive. Individual flight distances of the GPS-marked cows varied considerably, both in the calving season in June and during the hunting season. Combining both observation periods, some individuals consistently fled short distances, some individuals always fled long distances, while the flight distances of others varied much and inconsistently (Figure 1). When flushed in both periods, female moose had a mean flight distance of 1750 m, minimum 111 m and maximum 7326 m. The flight distance of one individual moose, ID 3210, varied from 184 m to 6879 m (Figure 1). There was no difference in flight distance between survivors and those shot during the hunting season after correcting for season and date.

When flushed in June the mean flight distance was 1364 m (min: 117 m, max: 7326 m) and it took on average 2 hours before they settled down. When flushed during the hunting season, the female moose fled a mean distance of 2338 m (min: 111 m, max: 6879 m) and it took on average 3 hours before settling down. Female moose fled a significantly shorter distance in June compared to during the hunting season (t_{30}=2.03, $p<0.050$; Figure 2).

During recreational hunting, female moose moved on average 1997 m (2SE=±121) per day on days without hunting and 2629 m (2SE=±216) on days when hunters were present. The linear model that related the log-transformed daily travel distance to hunting and date showed that female moose moved on average 1.16 times further on hunting days as compared to days without hunting (coefficient for days with hunt vs. non-hunt 0.147±0.041, $F_{27,1184}$=-5.89 $p<0.001$, Figure 3). Female moose moved further per day early in the hunting season regardless of hunting activity (coefficient -0.005±0.001, $F_{27,1184}$=3.52 $p<0.001$, Figure 3). All other variables were non-significant.

The expected distance moved per day when undisturbed was 3793 m. 16.6 % of the marked moose moved more than expected when there were hunters in the hunting unit and 10 % when there were no hunters in the hunting unit. The expected hourly distance moved was 158 m. Moose moved further than expected in 78.3 % of all cases during culling and 91.4 % of all cases during calf checking in June.

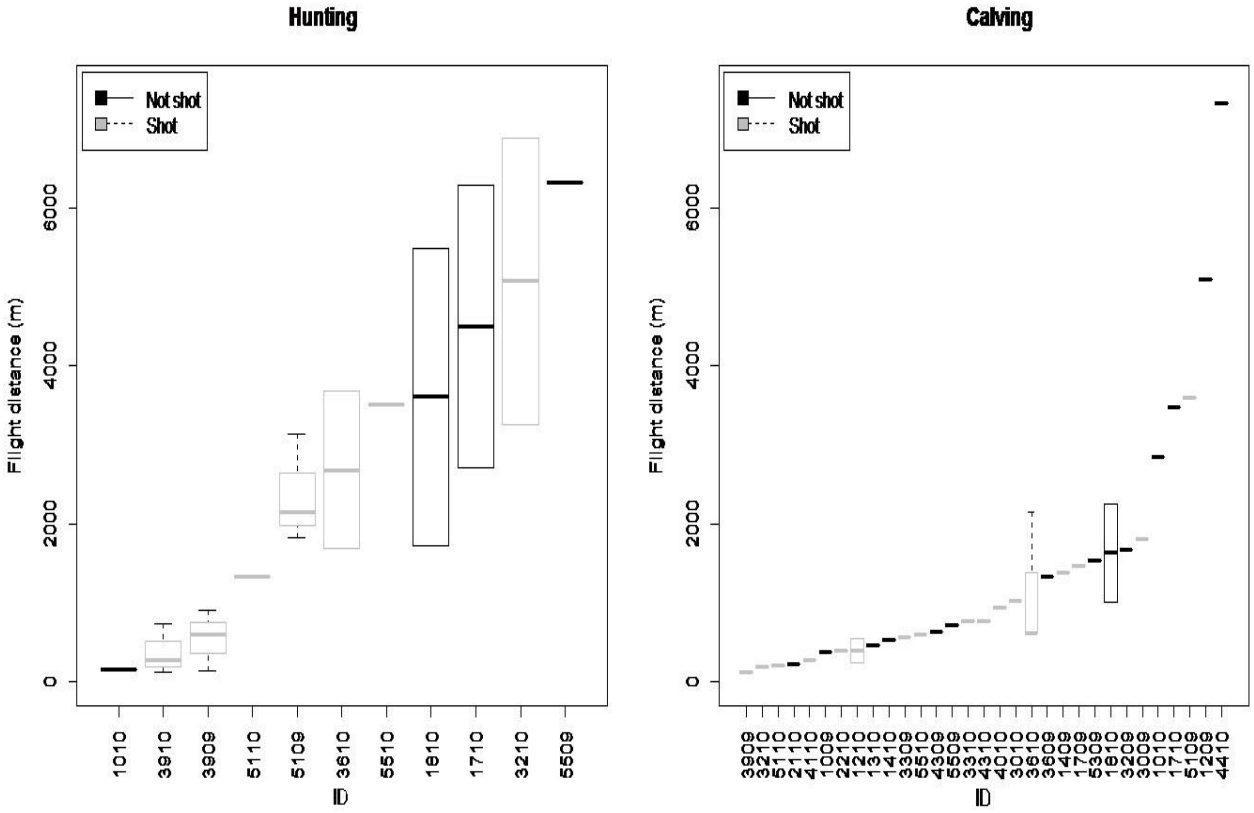

Figure 1: Flight distance for each of the individuals (ID) during the calving and hunting seasons. The bottom and top of the box are the lower and upper quartiles; the middle band is the median and the whiskers shows minimum to maximum distances. Individuals in grey got shot during the hunting season.

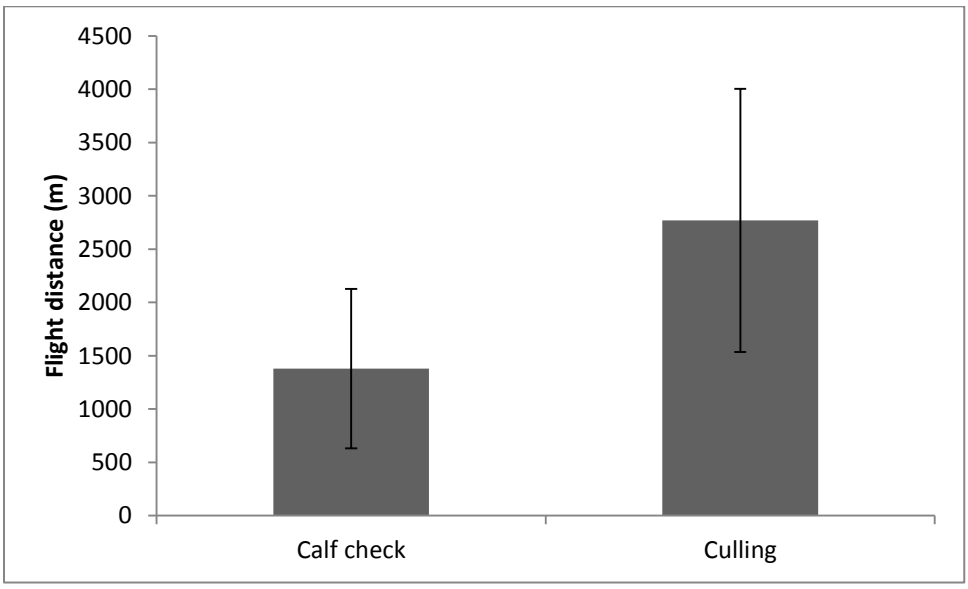

Figure 2: Average (±2SE) flight distances (m) during culling and calf checking

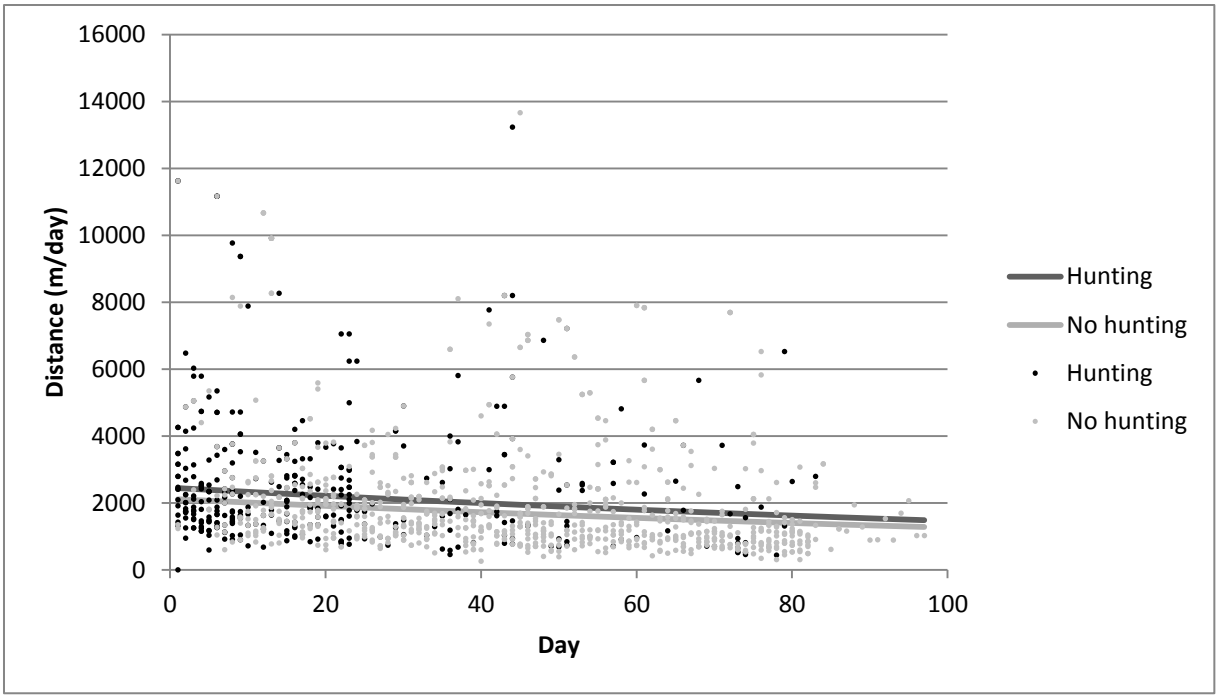

Figure 3: All observed (points) and predicted (lines) flight distances (m) during hunting and non-hunting days in the hunting season.

Discussion

Predators have different methods of attacking and killing prey. A moose in top condition can defend itself against some predators, but not all (Peterson, 1977). In the case of hunting by humans, this strategy is unlikely to be effective and I found no instances of this. Instead I found that moose avoided humans in all cases by run away or by sneaking away. Even though I did not find any cases where the moose stood still and were aggressive against humans, we know that they often do this against hounds when hunting with loose hounds. Furthermore, female moose fled further when disturbed in the hunting season than in the calving season, and showed greater movements on days when hunters were active in the area. There were considerable differences in individual flight responses, potentially influenced by an individual's previous experience, but no clear relationship between flight response and survival in the hunting season.

Although moose fled from humans during both the calving and hunting seasons, they fled further in the hunting season and had greater daily travel distances on hunting days. Ungulates in Norway should have learnt through evolution that humans are dangerous and that fleeing is the safest option. As humans have not been dangerous as predators for ungulates in the calving season since the Norwegian hunting law of 1899, this implies a response to temporal variation in human predation risk, as expected from the risk allocation hypothesis (Sönnichsen 2013). However, in the calving season moose calves are easy prey for other predators. On average, a bear takes 7.6 moose calves per calving season in

Scandinavia (Rauset, et.al, 2012) and wolves also show a strong selection towards moose calves during the summer (Sand, et.al, 2005). Calves of large game species restrict the movement of their mothers when they are very small and young (Grignolio, et.al, 2007; van Beest, et.al, 2011; Sönnichsen 2013). This is likely an important factor in the shorter flight distances in the calving season, but because of the high predation risk during the calving season and the constraint on flight distances of young calves, moose may also have learnt that instead of taking the risk of running from predators it is best to stand still and try to defend the calf in the calving season.

Individual moose showed different anti-predator behaviours when disturbed by humans. When culling specific individuals during the hunting season, 21.7 % of the radio-marked moose did not move more than expected, while in June 8.6% did not move more than expected. One of the females (ID 3909) used sneaking strategy in both seasons, but only in 50% of the chases during culling. During both seasons some of the moose (12 %) circled around instead of running away. Ciuti et.al, (2012) found that elk (*Cervus elaphus*) that were harvested increased their movement when the probability of encountering hunters was high, while elk that survived decreased movements and showed avoidance of open areas. I did not find any difference in the flight distance between moose that survived and those that were shot. This difference could be explained if we compare hunting methods in Norway and in Canada. In Norway moose hunters very often hunt in big groups and often use moose hounds, while in Canada they often use spotting scopes and binoculars before they approach the elk (Ciuti et.al, 2012). Most of the hunters in Canada use open terrain while hunting and therefore the elk are more likely to be shot in open terrain. In Norway all different terrain types are used during hunting, but especially forest.

If we compare predation by humans and wolves, there is different selective pressure due to different hunting methods (Proffitt, et.al, 2009). In North America, several studies have shown that prey species quickly regain their past anti-predatory behaviour when larger predators are reintroduced into an area from which they have been absent for a long period (Hunter and Skinner, 1998; Berger, 1999; Berger, et.al, 2001; Laundré, et.al, 2001). In Scandinavia where large predators have been absent for a long time, moose seem to be more naïve towards wolves compared to moose in parts of North America where wolves have always been present (Sand, et.al, 2006). I saw a wide variation in how individual moose behaved when hunted (Figure 1). This may partly be due to individual differences in personality and boldness (Cuiti et al. 2012).

When hunted by wolves, moose do not need to run far. The wolf chases on average 76 m for moose, with successful attacks occurring within an average of 66 m and unsuccessful attacks covering on average 123 m (Wikenros, et.al, 2009). Since 90% of wolf attacks on moose involve a chase of less than 400 m, the moose is likely to survive wolf attacks if it runs 500 m or more (Wikenros, et.al, 2009). North American moose are significantly more aggressive than Scandinavian moose, but the Scandinavian moose are more afraid of humans (Sand, et.al, 2006). My field experiences support this. During calf checking, I was never threatened by the female even if I came between her and the calf. In

these cases the female moose ran away when she noticed the observer. In North America, wolf hunting success on moose was 2.0-9.9 times higher than in Scandinavia (Sand, et.al, 2006). I found that moose had an average flight distance of 1750m. This means that most likely the moose will survive if they use the same anti-predator behaviour for wolves and managed to escape from the wolf within the first 500 meters. Peterson (1977) writes that moose are most likely to survive if they stand still and are aggressive against the wolf. During wolf attacks moose therefore can either stand still and be aggressive against wolves or run at least 500m from the wolf. By contrast, in a meeting with humans it is smartest to run. But despite their fear for humans, they only increased the distance moved by 1.16 when hunters were present in the hunting unit. If we look at hunting traditions in Norway we see that many hunters use loose dogs during the hunt and therefore many of the moose that are standing still and are aggressive to the dog will be killed. Also if a moose behaves aggressively towards humans in Norway and humans feel threatened, they will probably shoot the moose. I would therefore expect strong selection against the standing still strategy. This could be one of the reasons for the apparent naivety of moose towards wolves in Scandinavia.

In my study area an average moose hunting unit was 13.44 km^2. A circle with an area of 13.44 km^2 has a radius of just over 2 km. This means when moose are hunted by humans here it is profitable for them to run 2 km. They then get out of the hunting unit almost wherever they were and will then be safe from the specific situation, although they may risk encountering other hunters in the next hunting unit. I found a statistically significant difference in the daily travel distance between days with and without hunting, but the differences was not that big, both being around 2 km and therefore similar to the flight distance in the hunting season. From a management perspective, it therefore seems unlikely that the presence of hunters will affect the availability of moose in the area. In Norway the small game hunting season starts 10th September, 15 days before the moose hunt starts. Some moose-hunting landowners do not want small game hunters in the hunting unit before the moose quota has been filled, because they think small game hunters will scare the moose out of the hunting unit. Based on what I found it seems the moose will move about the same distance even though there are hunters in the hunting unit. Landowners that hunt moose need not worry about allowing small game hunters to hunt before the moose hunting season starts.

Acknowledgements

I want to thanks for the opportunity to join the project Improving moose forage with benefits for the hunting forestry and farming sectors at Hedmark University College, Evenstad. Big thanks to Torstein Storaas which has been brilliant supervisor and helped me a lot. I also want to thanks Jos Milner that has been helping me during the data sampling and to Barbara Zimmermann and Harry Andreassen that helped me with the statistics. Thanks to all landowners that let us hunt on the GPS-marked moose and to Tor Taraldsrud in Stor-Elvdal landowners association. Thanks to everybody that helped me during

the hunting, especially Snorre Fuske, Eivind Lurås, Alvar Hansen and Jon Inge Vik. And also thanks to Knut B Nicolaysen that let us borrow a combitrack. Funding was provided by Norwegian Research Council (173868/AREAL), Innovation Norway, Telemark County, Hedmark County and municipalities in Telemark, Vestfold and Hedmark All work carried out during this study conforms to the legal requirements set by "Forsøksdyrutvalget" (Animal Research Committee) in Norway.

References

Andersen, R., Linnell, J., & Langvaten, R. (1995). Short term behavioural and physilogical response of moose Alces alces to military disturbance in Norway. *Bilogical Conservation* 77, pp. 169-176.

Arnemo, J., Kreeger, T., & Soveri, T. (2003). Chemical immobilization of free-ranging moose. *Alces* 39, pp. 243-253.

Baskin, L., Ball, J., & Danell, K. (2004). Moose escape behaviour in areas of high hunting pressure. *Alces* vol. 40, pp. 123-131.

Berger, J. (1999). Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proc. R. Soc. B* 266, pp. 2261-2267.

Berger, J., Swenson, J., & Persson, I. (2001). Re-colonising carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science 291*, pp. 1036-1039.

Ciuti, S., Muhly, T., Paton, D., McDevitt, A., Musiani, M., & Boyce, M. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B-Biological Sciences*, 279(1746), pp. 4407-4416.

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray, Albemarle street.

Finnish Game and Fisheries Research Institute. (2012). Finnish Game and Fisheries Research Institute. Retrieved February 6 , 2013, from Annual game bag: http://www.rktl.fi/english/statistics/hunting/

Franzmann, A.W. (1981). Alces alces. *Mammalian species* No.154, pp. 1-7.

Franzmann, A. W., & Schwartz, C. C. (2007). Ecology and management of the north american moose. Second edition. Wildlife management institute.

Fritz, J. (2008). The effect of rut and hunting activity on movement in female moose with and without calves. Master thesis. Høgskolen i Hedemark avd. Evenstad.

Grignolio, S., Rossi, I., Bertolotto, E., Bassano, B., & Apollonio, M. (2007). Influence of the kid on space use and habitat selection of female Alpine ibex. *Journal of Wildlife Management*, 71, pp. 713-719.

Gundersen, H. (2003). Vehicle collisions and wolf predation: Challenges in the management of a migrating moose population in southeast Norway. Phd. University of Oslo.

Harvey, P. H., & Greenwood, P. J. (1978). Anti-predator defence strategies: some evolutionary problems. In Behavioral ecology: an evolutionary approach (ed. J. R. Krebs & N. B. Davies),

Hunter, L., & Skinner, J. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* 135, pp. 195-211.

Kozhechkin, V., Shishikin, A., & Tumanov, I. (2005). Moose (Alces alces) mortality caused by wolverines in the forest zone of Krasnoyarsk Territory, Russia. 1st International Symposium on Wolverine Research and Management: Agenda and Abstracts (pp. 22-23). http://www.carnivoreconservation.org/files/meetings/wolverine_2005_jokkmokk.pdf.

Laundré, J., Hernández, L., & Altendorf, K. (2001). Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park. *Can. J. Zool.* 79, pp. 1401-1409.

Lavsund, S., Nygrén, T., & Solberg, E. J. (2003). Status of moose populations and challenges to moose management in Fennoscandia. *Alces* vol. 39, pp. 109-130.

Lykke, J. (2005). Selective harvest management of a Norwegian moose population. *Alces* Vol.41, pp. 9-24.

Magoun, A., Carroll, G., Krebs, J., Lofroth, E., & Valkenburg, P. (2005). Wolverine predation on moose in North America. 1st International Symposium on Wolverine Research and Management: Agenda and Abstracts (p. 39). http://www.carnivoreconservation.org/files/meetings/wolverine_2005_jokkmokk.pdf.

Milner, J., van Beest, F., Solberg, E., & Storaas, T. (2012). Reproductive success and failure- the role of winter body mass in reproductive allocation in Norwegian moose. *Oecologia*, 10.1007/s00442-012-2547-x.

Neumann, W., Ericsson, G., & Dettki, H. (2009). The non-impact of hunting on moose Alces alces movement, diurnal activity and activity range. *Eur J Wildl Res* 55, pp. 255-265.

Odum, E. (1983). Fundamentals of ecology, 3rd. ed. New York: CBS College Publ.

Peterson, R. (1977). Wolf ecology and prey relationships on Isle Royale. US Natl Park Service *Sci. Monogr. Ser.* No. 11.

Proffitt, K., Grigg , J., Hamlin, K., & Garrott, R. (2009). Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. *J. Wildl. Manage*. 73(3), pp. 345-356.

R Development Core Team. (2009). R:A language and environment for sratistical computing. Retrieved from R Foundation for Statical Computing, Vienna, Austria. ISBN 3-900051-07-0: http://www.R-project.org

Rauset, G. R., Kindberg, J., & Swenson, J. (2012). Modeling Female Brown Bear Kill Rates on Moose Calves Using Global Positioning Satellite Data. *J. Wildl. Manage.* 76(8), pp. 1597–1606.

Rolandsen, C. M., Solberg, E. J., Bjørneraas, K., Heim, M., Mooter, B. V., Herfindal, I., et al. (2010). NINA Rapport 558: Elgundersøkelsene i Nord-Trøndelag, Bindal og Rissa 2005-2010. Trondheim: Norsk Institutt for naturforsking.

Root, B., Fritzell, E., & Giessman, N. (1988). Effects of intensive hunting on white-tailed deer movement. *Wildl.Soc.Bull.*16, pp. 145-151.

Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proc. R. Soc*. B 273, pp. 1421-1427.

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H., & Pedersen, H. (2005). Using GPS-technology and GIS-cluster analyses as tools to estimate kill rates in wolf-ungulate ecosystems. *Wildl. Soc. Bull*. 33, pp. 914-925.

Solberg, E. J., Saether, B.-E., Strand, O., & Loison, A. (1999). Dynamics of a Harvested Moose Population in a Variable Environment. *J. Anim. Ecol.* Vol. 68, No. 1, pp. 186-204.

Statistics Norway. (2012). Statistics Norway. Retrieved February 6, 2013, from Moose hunting. Preliminary figures, 2011/2012: Small increase in felled moose: http://www.ssb.no/english/subjects/10/04/10/elgjakt_en/

Storaas, T., Nicolaysen, K., Gundersen, H., & Zimmermann, B. (2005). Project Moose – traffic in Stor-Elvdal 2000-2004 – how to avoid moose-vehicle accidents on roads and railway lines. Hedmark University College, Evenstad.

Svenska Jägareförbundet. (2012). Svenska Jägareförbundet. Retrieved February 6, 2013, from Älgavskjutning: http://www.jagareforbundet.se/Viltet/Viltovervakningen/Algavskjutning/

Sönnichsen, L., Bokje, M., Marchal, J., Hofer, H., Jezdrzejewska, B., Kramer-Schadt, S., et al. (2013). Behavioural Responses of European Roe Deer to Temporal Variation in Predation Risk. *Ethology*, Vol.119, Issue 3, pp. 233-243.

Telfer, E. (1984). Circumpolar distribution and habitat requirements of moose (Alces alces). In R. Olson, R. Hastings, & F. Geddes, Northern ecology and resource management (pp. 145-182). Edmonton: Univ. Alberta.

van Beest, F., Rivrud, I., Loe, L., Milner, J., & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol*. 80, pp. 771-785.

van Beest, F., Van Moorter, B., & Milner, J. (2012). Temprature-mediated habitat use and selection by a heat-sensitive northern ungulate. . *Animal Behaviour*, 84., pp. 723-735.

Wabakken, P. (1986). Hvorfor finnes varg i Värmland? In Eles, H. (red), Vargen –Värmland förr och nu 1986. (pp. 29-35). Årbok Värmland Museum 84.

Wabakken, P., & Maartmann, E. (1994). Sluttrapport forbjørn-sauprosjektet i Hedmark 1990-93. Trondheim: NINA.

Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T. H., Flagstad, Ø., et al. (2012). Ulv i Skandinavia og Finland: Sluttrapport for bestandsovervåking av ulv vinteren 2011-2012. Elverum: Hedmark university college.

Wartiainen, I., Tobiassen, C., Brøseth, H., Bergsvåg, M., Aarnes, S. G., & Eiken, H. G. (2010). Populasjonsovervåkning av brunbjørn 2009-2012: DNA analyse av prøver samlet i Norge i 2009. Svanhovd: Bioforsk.

Wikenros, C., Sand, H., Wabakken, P., Liberg, O., & Pedersen, H. (2009). Wolf predation on moose nd roe deer: chase distances and outcome of encounters. *Acta Theriologica* 54 (3), pp. 207-218.