Norwegian University of Life Sciences

Preface

This thesis is written as the final paper of the master program in Natural Resource Management at the Norwegian University of Life Sciences. It is the product of a summer in the field, and a five month writing and analysis period.

I would like to extend my gratitude to my supervisor Dr. agric. Olav Hjeljord for his efforts in guiding me onto the right path, and aiding and organizing in my field work. I would also like to thank him for calling every day at 9 o'clock during my field work, securing that I woke up at a decent time. I would also like to thank everyone who helped me in finding the appropriate sites for data collection; Marnardal kommune, the forest owners of Vegårshei, Fritzøe Skoger, Sande kommune, Stangeskovene, Rakkestad kommune, and Åsnes commune.

For continuing social support and welcome distractions I must thank the "Coffee Club"; Dag, Runar, Ole-Jakob, Heidi, Eirin, Torbjørn, Henriette, and Silje. Finally, a thank you to my girlfriend Martha Andrea for keeping me happy and taking my mind off frustrating days in front of the computer.

Ås, May 14th 2013

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Fridtjof Denneche

Abstract

There has been a recorded difference in carcass weights among moose (*Alces alces*) on the western side of the Oslo fjord compared to the eastern side over the last decades. So far, this reduction has been credited to density-dependent limitations in browse availability leading to a higher browsing pressure. I compared browse availability and pressure on clearcuts in two ranges with differences in moose fitness. I found that the western ranges have more preferred browse, but I did not find a significant difference in the availability of birch (*Betula spp.*). Browsing pressure was significantly higher in the east on older clearcuts, but the difference disappeared on younger clearcuts. In the east, older clearcuts were more heavily browsed than younger, but this was not the case in the west. This study concludes that browse availability today is not the reason for the difference in carcass weights. The problem must therefore rest with the western moose population, and needs further investigation. A culling of the population in a trial area could be conducted to further investigate this matter, or we have to wait until the fertile of the 1950's sites that led to the increase in moose fitness then, are logged again.

Sammendrag

De siste tiårene har det vært notert en forskjell i slaktevekter hos elg (*Alces alces*) på vestsiden av Oslofjorden sammenliknet med østsiden. Så langt har denne forskjellen vært tilskrevet tetthetsavhengige begrensninger i beitetilgjengelighet som har ledet til høyere beitetrykk. Jeg sammenliknet beitetilgjengelighet og –trykk på hogstflater i to områder med forskjeller i elgkondisjonen. Jeg fant at det vestlige området har mer foretrukket beite, men kunne ikke finne en signifikant forskjell i forekomsten av bjørk (*Betula spp.*). Beitetrykket var signifikant høyere i øst på eldre hogstflater, men forskjellen forsvant på yngre flater. I øst var eldre flater hardere beitet enn eldre, men dette var ikke tilfellet i vest. Jeg konkluderer med at beitetilgangen ikke er årsaken til forskjellen i slaktevekter. Problemet må derfor ligge hos elgbestanden i vest, og dette trenger ytterligere forskning. En kraftig avskyting av bestanden i vest kan gjøres i et prøveområde for å se om slaktevektene øker, alternativt må man vente til flatene som ble hogget på 1950-tallet og førte til oppgangen i bestanden da, blir hogget igjen.

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Introduction

Since the 1950's, the moose population in Norway has increased dramatically (Solberg et al. 1999). Along with this growth there has been recorded a reduction in moose body weight and reproduction rates along with other signs of poor health, such as fragile bones and kidney damages (Bjerga & Mysterud 1999). This reduction in moose fitness has been recorded mainly on the western side of the Oslo fjord and has so far been credited to density-dependent food limitations (Bjerga & Mysterud 1999; Hjeljord 2008). However, despite the same general increase in population size, the condition of moose on the eastern side of the Oslo fjord has not experienced the same reduction in health and body mass. To reduce the density of moose and thereby increase the condition it was harvested heavily on the western side of the fjord and the population has been reduced by 30-50% since the population peak around 1990 (Hjorteviltregisteret 2013a). Despite this population reduction, the condition of moose in these areas has not improved, rather continued to get worse, albeit at a slower rate.

Concurrent with the reduction in moose density, there has also been a change in timber harvest. More timber is now harvested through thinning and selective logging, than clearcutting (Wam et al. 2010). Furthermore, when clearcutting was first introduced to these regions, the sites of highest soil fertility was generally logged first and sites of progressively lower fertility logged as time progressed. As the most abundant browse is produced on clearcuts of high soil fertility (Niemela & Danell 1988; Wam & Hjeljord 2010a), logging may have led to less browse in recent years compared to the previous years. Together with heavy browsing this may mean that, although the moose population has been reduced, browse availability has been reduced even more and is the cause of continued decrease I body condition.

Another possibility could be that there has in fact been an improvement in browse availability relative to moose density. However, because moose condition and reproductive performance are slow to respond, the expected improvement may still take several years.

To investigate which of the two hypotheses are most likely to be true, I compared browsing pressure and browse availability on the western ranges with the eastern ranges. If browse availability is less, and browsing pressure higher on the western ranges compared to the eastern ranges, this may indicate that the moose population on the western ranges is still too high in relation to browse availability. If merely, the response by the moose population is slow, little may be gained from further reduction of the population. To investigate the historic browsing pressure more precisely, I compared old and new clearcuts between the two ranges and put forth the following hypothesis: If there has been no change in browsing pressure over time, we would expect the relative browsing pressure to be the same on young and old clearcuts when we compare east and west. If browsing pressure has decreased in the west in recent years due to reduce moose density, we would expect relative lower browsing pressure on young clearcuts compared to the east. If the latter is true, the problem of low increase in condition must rest with the moose population.

Background

Moose is the largest species in the *Cervidae* family. After arriving in Norway after the last ice age, it is now found in all of Norway, except from some areas on the western coast, and in the coastal areas of the very northern Norway (Bjärvall & Ullström 1997).

Since the late 1800's the number of moose shot has been registered on Norway. At the end of the 19th century, the moose population was at a low point. This was due to modern and more efficient hunting methods along with a high wolf population and increased grazing by domestic animals (Hjeljord 2008).

After World War 2 the population increased, and so did the hunting efforts. From shooting around 1 000 animals per year before the war, the harvest reached its peak in the late 20th century with between 35 000 and 40 000 animals shot per year (Bjärvall & Ullström 1997; Statistics Norway 2013a). After introducing a new law on game in 1951, the old practice with one moose allowed shot per property with forest or other uncultivated areas was replaced with hunting quotas set by the department of agriculture (Skavhaug 2005). These quotas were conservative, and the moose population kept on increasing on a national basis (Hjeljord 2008).

This story was generally similar around the Oslo fjord until the late 1980's. Thereafter, the eastern population reached equilibrium, whereas the western population has experienced a decline. (Hjorteviltregisteret 2013c; Statistics Norway 2013a). The increased harvest was due to the desire to aid the moose in recovering from the poor conditions and lower body mass (Solberg et al. 2006), by now the harvest is reduced by around 50% (fig. 1).

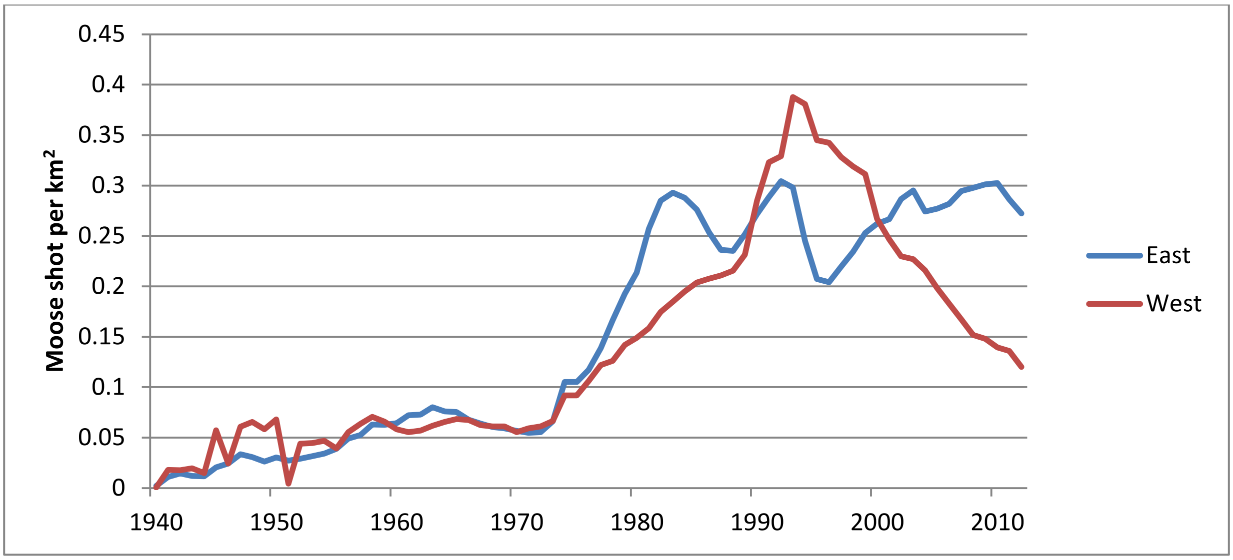

Figure 1: Number of moose shot per square kilometer in eastern range (Østfold, Hedmark and Akershus) and western range (Vest-Agder, Aust-Agder, and Vestfold) from 1940 to 2012 (Statistics Norway 2013a).

Study populations

There has been recorded a difference in carcass weights of moose between the eastern and western side of the Oslo fiord (Hjeljord 2008). Carcass weights are defined as the weight of the skinned animal, from which the viscera, head, and lower legs has been removed (Sæther & Haagenrud 1983). Average carcass weights are generally higher in the eastern ranges, along the Swedish border. In our study populations the average carcass weights are higher for all age classes in the east (fig 2, 3, 4).

Data on carcass weights are collected from the national database on cervids, Hjorteviltdatabasen (www.hjortevilt.no). The database is comprised of data from hunters and are collected and quality controlled by municipalities (Hjorteviltregisteret 2013b).

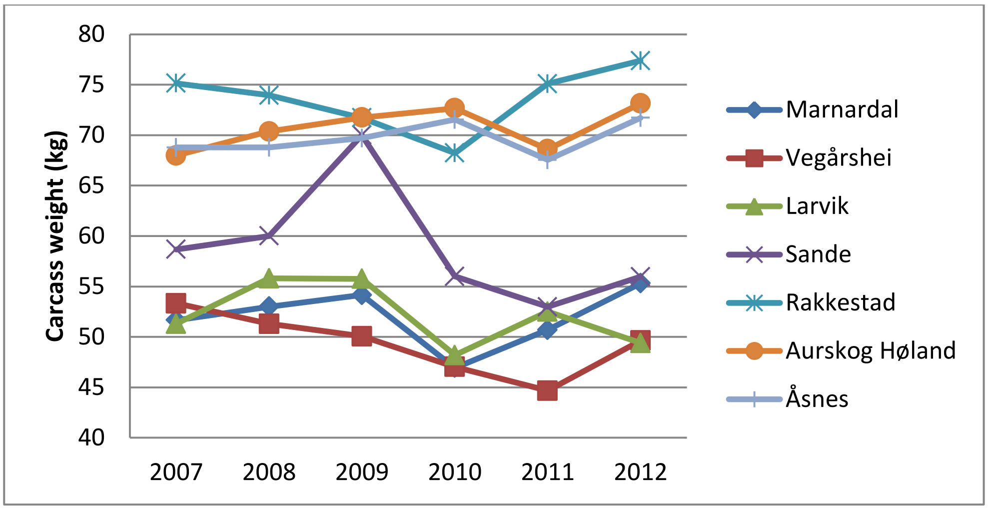

Figure 2: Average carcass weight of calves in seven Norwegian moose ranges between 2007-2012 (Hjorteviltregisteret 2013a).

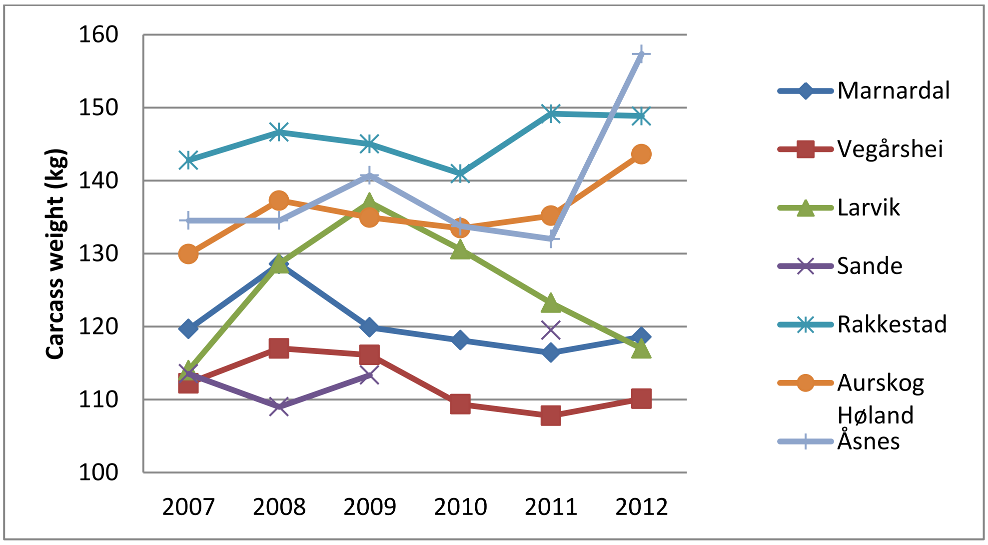

Figure 3: Average carcass weight of yearlings (1.5 years old) in seven Norwegian moose ranges between 2007 – 2012 (Hjorteviltregisteret 2013a).

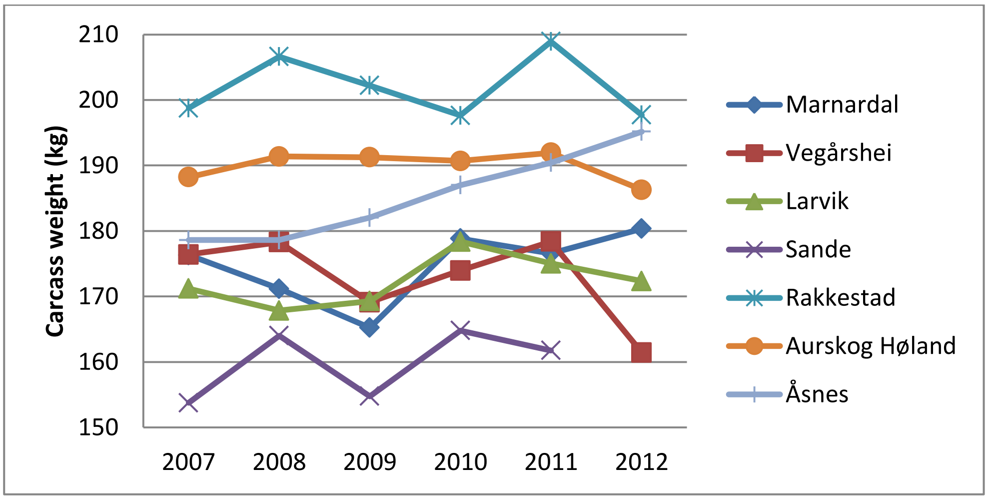

Figure 4: Average carcass weight of adult animals in seven Norwegian moose ranges between 2007 – 2012 (Hjorteviltregisteret 2013a).

Methods

Study area

The study area is comprised of seven general areas in south-eastern Norway. These areas are in seven different counties and include the municipalities Marndardal (58°12'72" N, 7°30'48" E), Audnedal (58°17'18" N, 7°21'21" E) Vegårshei (58°44'57" N, 8°51'41" E), Gjerstad (58°52'45" N, 9°1'00" E), Andebu (59°18'21" N, 10°10'37" E), Stokke (59°13'19" N, 10°18'01" E), Larvik 59°03'03" N, 10°02'06" E), and Sande (59°35'37" N, 10°12'28' E) on the western side of the Oslo fiord (from now referred to as "western ranges"), and Rakkestad (59°25'43" N, 11°20'37" E), Aurskog-Høland (59°53'00" N, 11°34'00") and Åsnes (60°36'50" N, 12°00'50" E) on the eastern side ("eastern ranges"). The areas lie within the boreal forest zone and are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The occurrence of deciduous trees such as birch (*Betula spp*.), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and *Salix spp.* such as goat willow (*Salix caprea*) is also significant. Forest management is intensive in both ranges. Mature stands are harvested according to the law on forestry of 2005 (Lovdata 2009) and agreed standards. Although the initiative setting these standards has been discontinued, they are still followed (Levende Skog 2010). Regeneration time is normally between 80-120 years. The study areas are selected based on their location in different moose ranges, and the subsequent difference in moose condition.

Data collection

Both ranges were surveyed over the course of the summer season of 2012, from the 3rd until the 15th of July in the west, and from then until the 5th of August in the east. Within each municipality, 12 clearcuts were selected at random in cooperation with regional forest supervisors. Six are young (5-7 years old) and six are older (around 15 years old). When more than six relevant clear cuts were available, the sites were selected based on the distance from drivable roads, but care was taken to avoid clear cuts close to each other. The age of the clear cuts is based on reports provided by the local forest service. I chose to examine the two age classes because it gives me the ability to see if there have been changes in browsing pressure over time.

The data was collected using line transects across clear cuts. Every ten meters (paced by steps), a circular plot with a radius of 1.5 meters was laid out and the number of birch, rowan, aspen, goat willow, other *Salix spp.*, oak (*Quercus spp.*), bird cherry (*Prunus padus*), juniper (*Juniperus communis*), Scots pine, and others was counted. On each clearcut, I laid out 30 plots (n=2520). Browsing pressure on rowan, aspen and goat willow was not registered, as these species are heavily browsed on both ranges (Wam & Hjeljord 2010b). Birch constitute the main part of the moose diet in this study area (Conradi 2011) and is therefore commonly chosen as a measure of browse availability. Although it is shown that moose prefer *B. pendula* to *B. pubescens* (Danell et al. 1985), both species are registered as birch. *B. pendula* dominate on the western region, and *B. pubescens* dominate in the east (Conradi 2011). To examine the browsing pressure, birch was divided into four classes (table 1).

Table 1: Criteria for determination of browsing pressure on birch

Class	Criteria for determination of browsing
Class 1	Not browsed or maximum two twigs browsed
Class 2	Medium browsing. More than two twigs browsed, but no sign prevention of height increment. ("hedging")
Class 3	Severely browsed. Visible "hedging".
Summer	Leaves removed the summer of the field work.

The average height of birch trees was noted for each plot, and the average height of coniferous trees were noted per clear cut. Trees lower than 30 centimeters and higher than three meters are excluded from the data, due to their height, which makes them unavailable for moose browsing (Hjeljord et al. 1990). Roe deer (*Capreolus capreolus*) is sympatric with moose in all ranges of this study, and red deer (*Cervus elaphus*) was observed in the south-westernmost municipalities Marnardal and Vegårshei. However, as their density is low, it is believed that they are not a source of significant bias in the data (Wam & Hjeljord 2010b).

Data analysis

The data was averaged per clear cut and organized using Microsoft Excel and the statistical analysis was done with R (www.r-project.org). I analyzed the difference in browse availability between the two ranges using welch two sample t-test. Furthermore, the difference between the two ranges was analyzed on younger and older clearcuts. I also analyzed the difference in browsing pressure between the eastern and western ranges using welch two sample t-test. To determine a statistical difference between the ranges, the significance level is set to p=0.05.

Results

Browse availability

There was no significant difference in density of birch between east and west albeit there was a trend of higher density in the east. For the preferred species rowan, aspen and goat willow, the density was significantly higher in the west (table 2).

Table 2: Average number of trees in two Norwegian moose ranges (7°21'E - 12°00'E) surveyed in 2012. Two way t-test between ranges.

Species	East	West	t-value	Df	p-value
Birch (*Betula spp.)*	59.33	49.89	0.7013	76.807	0.485
Rowan	5.83	27.21	-4.6817	58.369	**<0.001**
Aspen	0.92	7.13	-2.5572	49.085	**0,014**
Goat willow	0.31	2.55	-3.1476	48.284	**0,003**
Other *Salix spp.*	0.33	0.87	-0.9483	51.678	0.347
Oak (*Quercus spp.)*	0.00	2.38	-3.1201	46	**0.003**
Bird cherry	0.00	0.02	-1	46	0.323
Common juniper	0.00	5.23	-1.9387	46	0.059
Scots pine	16.78	10.40	0.9262	49.345	0.058
Other	28.03	28.94	-0.1618	80.996	0.872

On younger clear cuts, there are a higher number of birch trees in the east (30.88) than in the west (24.74). However, this trend is not significant ($t = 0.8985$, $df = 38.423$, $p = 0.188$). On the older clear cuts, the average number of birch trees in the east is 87.78, and 74 in the west ($t = 0.594$, $df = 37.959$, $p = 0.278$). On younger clear cuts an average of 27.43 birches were counted, and 79.9 were counted on older clear cuts ($t = -4.3728$, $df = 48.286$, $p = <0.001$).

Browsing pressure

The proportion of browsed birch trees (class 2 or higher) on young and old clear cuts combined tend to be higher in the east; 20.78% in the east compared to 14.37% in the west ($t = 1.4544$, $df = 57.729$, $p = 0.076$). The trend towards higher browsing in the east continues when browsing is compared between classes. In class 2 the average in the east is 17.81%, and 12.19% in the west ($t = 1.3898$, $df = 56.676$, $p = 0.085$). In class 3 the proportion is significantly higher in the east (1.17%) against 0.38% in the west ($t = 1.7408$, $df = 44.512$, $p = 0.044$). The proportion of trees browsed during the summer is evenly distributed between eastern and western clear cuts (1.8% in both east and west) ($t = 0.0028$, $df = 78.768$, $p = 0.499$) (fig. 5).

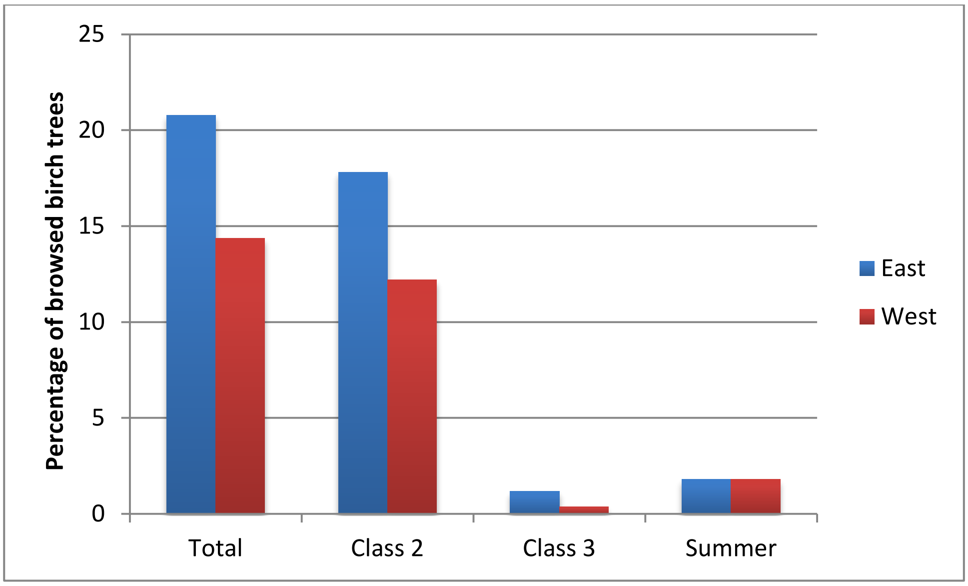

Figure 5: Average proportion of browsed birch trees in two Norwegian moose ranges (7°21'E - 12°00'E) surveyed in 2012.

Older versus younger clearcuts

The proportions of browsed birch trees tend to be higher on older, compared to on younger clearcuts, although not significantly (19.77% on older clear cuts vs. 14.47% on younger) ($t = 1.2759$, $df = 76.914$, $p = 0.103$). The trend continues with 17.24% on older clear cuts in class 2 against 11.96% on younger clear cuts ($t = 1.3935$, $df = 77.303$, $p = 0.084$). In class 3 the average is significantly higher on the older clear cuts (1.15%) against 0.28% on younger clear cuts ($t = 2.1652$, $df = 52.268$, $p = 0.017$). Summer browsing tend to be higher on younger clear cuts (2.23% versus 1.38%), but not significantly ($t = 0.8736$, $df = 62.344$, $p = 0.193$) (fig. 6).

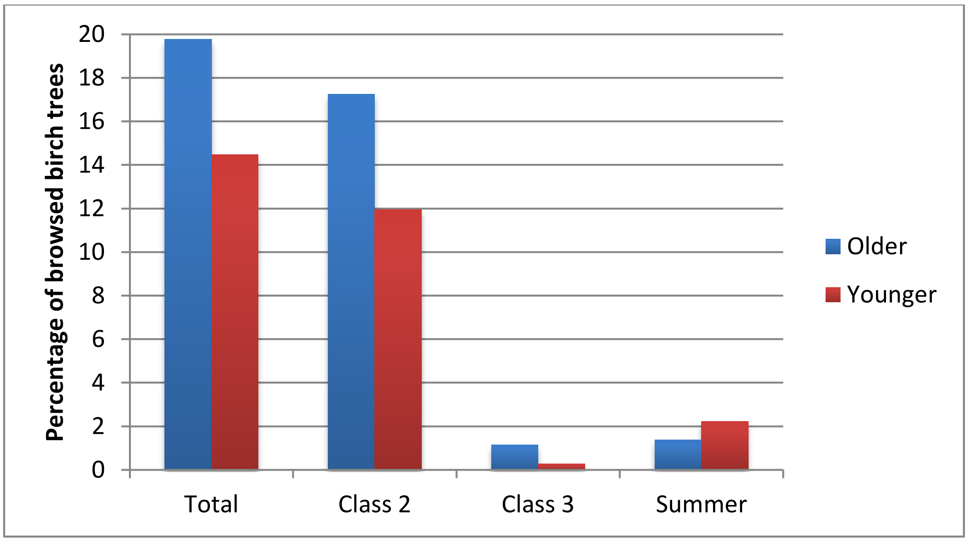

Figure 6: Average proportion of birch trees browsed on older (15-17 years) and younger (5-7 years) clear cuts in two Norwegian moose ranges (7°21'E - 12°00'E) surveyed in 2012.

Older clearcuts east and west

I found that there is a significantly higher proportion of trees browsed on older clearcuts in the east (29.93%) compared to those in the west 12.15% ($t = 2.6196$, $df = 20.753$, $p = 0.008$). In class two, the average is 25.67% in the east and 10.91% in the west ($t = 2.3459$, $df = 20.407$, $p= 0.015$). In class three the average is 2.19% in the east and 0.37% in the west ($t = 2.2802$, $df = 19.777$, $p= 0.017$). The averages of summer browsing are more similar. In the west an average of 0.87% of the trees are browsed and in the east 2.06% ($t = -1.2048$, $df = 28.501$, $p = 0.238$) (fig. 7).

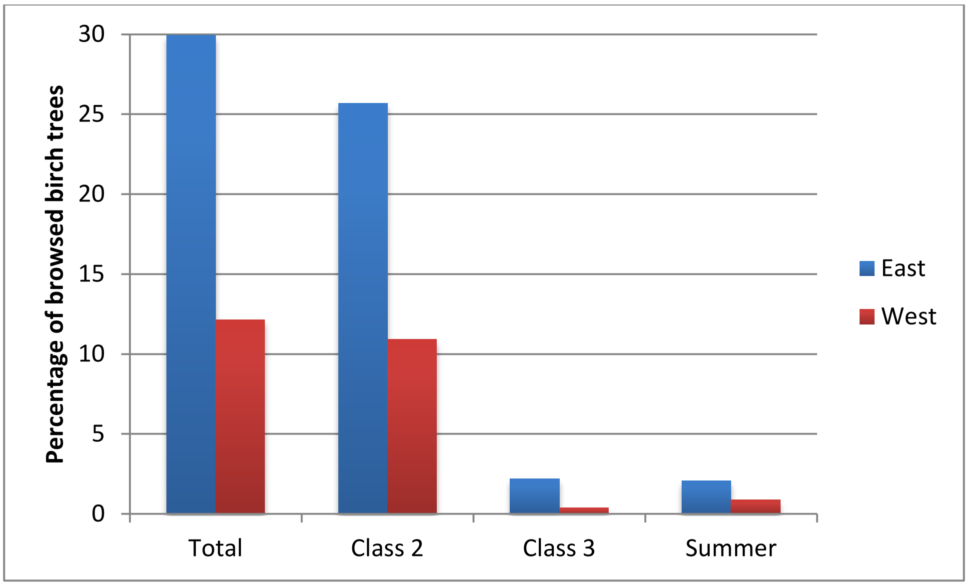

Figure 7: Average proportion of birch trees browsed on older (15-17 years) clear cuts in two Norwegian moose ranges (7°21'E - 12°00'E) surveyed in 2012.

Younger clearcuts east and west

On younger clear cuts the differences are not significant in any of the classes, but the averages tend to be slightly higher in the west. In total, the average of trees browsed on younger clearcuts in the west is 16.69% and 11.64% in the east ($t = 1.0316$, $df = 37.864$, $p= 0.154$). In class two the average in the west is 13.52% and 9.95% in the east ($t = 0.7831$, $df = 38.415$, $p= 0.219$). In class three the western clearcuts have an average of 0.4% of trees browsed and the eastern clearcuts have an average of 0.14% ($t = -0.9701$, $df = 35.25$, $p = 0.339$). Summer browsing is of a similar pattern, with western clearcuts averaging 2.77% against the eastern clearcuts averaging 1.54% ($t = 0.7333$, $df = 38.992$, $p= 0.234$) (fig. 8).

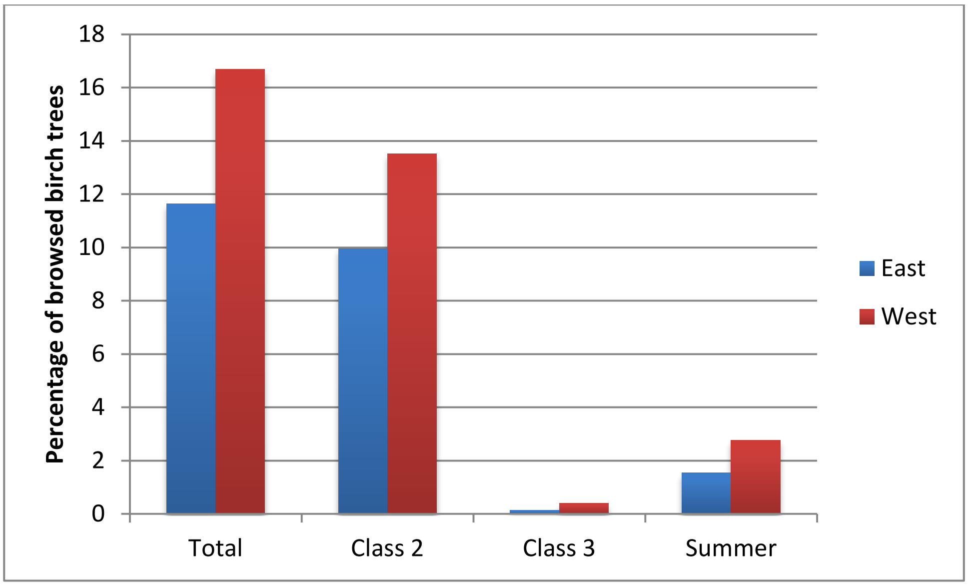

Figure 8: Average proportion of birch trees browsed on younger (5-7 years) clear cuts in two Norwegian moose ranges (7°21'E - 12°00'E) surveyed in 2012.

Browsing pressure within the ranges

When examining the browsing in the eastern range, I found that 29.93% of all birch trees were browsed on older clearcuts, compared to 11.63% on younger ($t = 2.5897$, $df = 23.607$, $p = 0.016$). The difference is also significant in class 2, where 25.67% birches on older clearcuts fall into this class, compared to 9.95% on younger ($t = -2.3758$, $df = 24.01$, $p = 0.026$). For class 3, 2.19% of all birches were hedged on older clearcuts, whereas only 0.14% were browsed on younger clearcuts ($t = -2.6263$, $df = 18.105$, $p = 0.017$). There is no significant difference between older (2.06%) and younger (1.54%) clearcuts in the east ($t = -0.3726$, $df = 31.8$, $p = 0.712$) (fig. 9a) when it comes to summer browse.

In the western range, there is no significant difference in the browsing pattern between older and younger clearcuts. On older clearcuts, 12.15% of all birches were browsed, compared to 16.69% on younger clearcuts ($t = -1.0108$, $df = 33.965$, $p = 0.319$). In class 2 13.52% of the birches are browsed on younger clearcuts, compared to 10.91% on older ($t = 0.641$, $df = 33.414$, $p = 0.526$). 0.4% of the trees on younger clearcuts are hedged compared to 2.19% on older ($t = 0.0891$, $df = 44.881$, $p = 0.929$). Summer browsing was 2.77% on younger compared to 0.87% on older clearcuts ($t = 1.4078$, $df = 29.05$, $p = 0.170$) (fig. 9b).

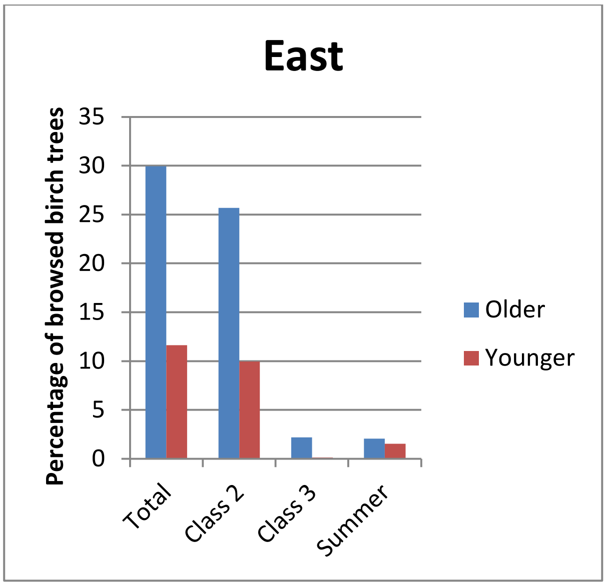

Figure 9a: Browsing pattern on birch in Østfold, Akershus and Hedmark, surveyed in 2012.

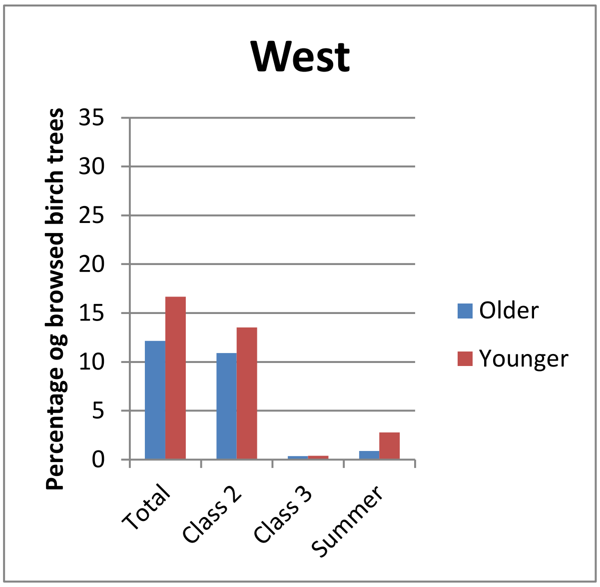

Figure 9b: Browsing pattern on birch in Vest-Agder, Aust-Agder and Vestfold, surveyed in 2012.

Discussion

I found no significant difference in the occurrence of birch between the eastern and western ranges (table 2). For the more preferred species rowan, aspen and goat willow, I found significantly more of these species in the west. Of all available browse species, birch was the most abundant on both ranges.

When investigating browsing pressure on birch, I found that the overall trend is towards a higher browsing pressure on birch in the east (fig. 5). Since I separated the younger and older clearcuts, I am able to determine whether there has been a change in the browsing pressure over the last 15 years. Overall, the browsing was more frequent on older clearcuts compared to younger (fig 6). This is expected as they have had longer time to be exposed to moose browsing. Between the ranges, older clearcuts were significantly more browsed in the east compared to the west (fig 7). When investigating younger clearcuts, I found that the trend has shifted towards a higher browsing pressure in the west, albeit, the difference is not significant (fig 8). Within the ranges, I found the expected trend that older clearcuts were significantly more browsed than younger in the east, but the trend was different in the west (fig. 9a, 9b).

The "range quality hypothesis", set forward by Hjeljord & Histøl (1999) states that the moose ranges will deteriorate as less preferred species such as birch become more common in the diet. Following this, animals who live in areas with a high abundance of preferred forage should have a higher body mass and fitness (Wam & Hjeljord 2010a). The results in this and other studies do not support this. The moose in the eastern study areas have a high body mass, although they have less preferred browse available and live mostly on a diet of birch of medium preference (Conradi 2011; Wam et al. 2010).

Overall availability of birch

This study does not support the hypothesis that low browse availability today is the reason for the reduced carcass weights in the western range. Previous studies done on browse availability and utilization in the same areas indicate similar findings (Conradi 2011; Rønning 2001; Wam et al. 2010), albeit in the studies of Conradi (2011) and Wam et al. (2010) the occurrence of birch in the east compared to the west was significantly higher. On the other hand, Rønning (2001) found no significant difference in the distribution of birch between the ranges. It is however, worth noting that there are some differences between the methodology in these studies and mine. Whereas I counted individual trees, Wam et al. (2010) used "the average length of current year's growth on an unbrowsed shoot" to measure browse availability. The study by Wam et al. (2010) also did not examine browse exclusively on clearcuts, but instead laid their transects across entire municipalities, but concluded that clearcuts had the most abundant browse. The same was done by Rønning (2001), but he used the same indicator as this study to estimate browse availability. Conradi (2011) essentially had the same methods as this study, but also used tree height to estimate browse density. Tree height could be argued to be a factor in the quality and abundance of browse, but since this study distinguishes between younger and older clear cuts, I am able to circumvent this issue by being able to see if there are differences on browse abundance between the older and younger clearcuts. In addition, the shoots in the upper part of the tree crown with the best access to sunlight generally are of better quality than shoots in the lower part of the crown (Hjeljord 2008). Therefore, height of the birch trees should not influence the overall quality of the browse.

Browsing pressure

The reason for the deteriorating moose population in the western range has been debated. Since birch today is the main part of the moose diet in both ranges and preferred browse like rowan, aspen and *Salix spp.* is equally heavily browsed on both ranges (Conradi 2011), I focused on birch in my analysis of browsing pressure.

My results show that birch previously tended to be more browsed in the eastern ranges (fig. 5), although this trend is not significant, except among the hedged birches (class 3). This is similar results to what was found by Wam et al. (2010), but in their case, the overall difference between the two ranges was significant. However, they did not grade the level of browsing per tree. Conradi (2011) and Rønning (2001) found different results, where birch tended to be more browsed in the west. The share of browsed birch recorded by Conradi (2011) is much higher than this study with around 70% of available trees browsed. The reason is probably that I judged trees with two or less than two twigs browsed as not browsed, whereas Conradi (2011) judged any tree with browsed twigs as browsed. The significant difference between the ranges in hedged trees can indicate that the browsing pressure has in fact been higher in the east.

Since this study distinguished between younger and older clear cuts, a change in the browsing pressure over time will be more apparent compared to previous studies where all clearcuts have been treated as equal. Studies have pointed out that condition and population performance can reflect the past rather than the present conditions (Monteith et al. 2009; Skogland 1994). My results show that there has in fact been a change in browsing pressure between older and younger clearcuts, where the older clearcuts showed a significant difference between the ranges. Eastern clearcuts were significantly more browsed, indicating that browse availability during this earlier period has in fact been better in the west than in the east. When considering this, and the higher availability of rowan, aspen and goat willow, the western moose population should have been able to regain some of the low body mass. Apparently this has not been the case. We could also expect that the moose in the eastern ranges would be affected by the higher browsing pressure in the past. This effect has yet to be seen, indicating that the browsing pressure has not been high enough to affect the population.

It is interesting that the browsing pattern is different between the ranges. In the eastern range, I found a significant difference in the browsing pressure between younger and older clearcuts.

This is not unexpected, since older clearcuts have been browsed over a longer time. However, the pattern is not the same in the west, where there is no significant difference in browsing pressure between older and younger clearcuts. I would expect that the pattern should be more similar to that in the east. If we treat the browsing pattern in the east as a control sample, we would expect browsing pressure on younger clearcuts in the west to be about a third of that on older clearcuts (fig. 9a, 9b). My results show that it is almost four times as high as we would expect it to be (fig. 9a, 9b). If we compare the harvest pattern between the two ranges (fig. 1), we see that the eastern ranges were more intensely harvested in the late 1970's and 80's. The western range increased its harvest around 1990, but the range had probably already become overbrowsed. I believe that the culling of the moose population in the west was started too late. The clearcuts in this study are not old enough to show this overbrowsing, and the effects are therefore not apparent. The square kilometers logged are not registered, but some large private forest owners such as Fritzøe Skoger in Vestfold have these numbers available (Milner et al. 2012). There has been a decline in total available clearcuts in some areas, and this trend appears to continue (Milner et al. 2012). Probably, also sites with lower soil quality are logged in this area today compared to earlier times. We would expect a higher browsing pressure in the east since the population is larger here (Hjorteviltregisteret 2013c), but since the sites in the east have a more even site quality (Wam et al. 2007), more sites can be logged and browsing could be less concentrated (fig. 9a, 9b).

Why is moose fitness low in the West?

Since the eastern moose population has maintained a high body mass despite higher browsing pressure it is still an open question why the western moose has not been able to regain the high body mass and increase its fitness. Earlier research on moose populations shows that there are several factors that contribute to determine moose fitness. Climate, geographical location, topographical conditions, and predation can all influence the fitness of a moose population in addition to human influences (Hjeljord & Histøl 1999; Mech et al. 1987; Musante et al. 2010; Solberg et al. 1999; Sæther 1985). Areas with favorable climatic condition will produce high quality forage and result in larger body mass (Hjeljord 2008). Several studies (Hjeljord & Histøl 1999; Sæther 1985; Sæther et al. 1996), claim that moose that inhabit areas with deep snow will have lower body mass in the following summer. Given that the average mid-winter snow depth is higher in the western ranges than the eastern (Met.no 2013), this can contribute to the difference in body mass (Hjeljord et al. 2000). Also, flat areas are more favorable than steep slopes (Hjeljord & Histøl 1999) and this fits well with the study area, where the eastern counties are flatter than the western.

It is also shown that tick-borne fever can have fatal consequences for moose (Jenkins et al. 2001; Musante et al. 2010). As the forest tick (*Ixodes ricinus*) is most abundant in the western range (Jore et al. 2011), this can influence on the moose population, although Milner & van Beest (2012) were unable to find any effects in their study. Given the effects on domestic animals and other ungulates (Samuel & Welch 1991; Stuen et al. 2002) further research should be conducted on this area.

Keech et al. (2000) showed that cows with a higher body mass produced larger offspring, and that this had a significant effect on the reproduction and life history of the next generations. Twin births are suggested as a measure of condition, and it is shown that twinning rates are higher when conditions are favorable (Franzmann & Schwartz 1985).

We can imagine that the lower birth weights and subsequent poorer condition affects the moose population over time as it does in reindeer (*Rangifer tarandus*) (Skogland 1994). Although little data exist on the ability of moose to rebound from low body weights, it is shown that populations can respond positively to improvements in browse availability and reduced competition (Bontaites & Gustafson 1993; Sinclair et al. In Press). Monteith et al. (2009) claim that there is a potential for time lags in responses of populations to improved environmental conditions. The study done by Bontaites & Gustafson (1993) and Musante et al. (2010) can be relevant in our case, the conditions in their studies were extremely favorable for an increase in both population numbers and body mass. The increase in their population was due to increased logging activities, lower intra-specific competition from white tailed deer (*Odocoileus virginianus*), and strict hunting quotas, with all of these occurring over several breeding seasons.

In addition to the above mentioned cohort effects, there can also have been a change in the occurrence of preferred browse. In the 1970's and 1980's when the western moose population experienced the biggest incline in numbers, the forest growth was also high (Statistics Norway 2013b). After clearcutting, species such as rowan, aspen and *Salix spp.* flourish, providing higher quality browse (Hjeljord 1980). As a result of less clearcutting, the forest is now closing and the high quality moose browsing areas are diminishing. After this period with high levels of clear cutting, the productivity and carcass weights have remained stable in the eastern ranges, but have decreased in the western. I assume that the most fertile stands are logged first, and subsequently stands of lower site quality are logged. After a cycle of 80-120 years, the sites are logged again (Edenius et al. 2002). In areas with varying site quality, such as the western range, I assume that the moose population will follow these cycles. The eastern range has a more homogenous site quality (Wam et al. 2007), so I do not assume the cycles to be as marked.

Even if we take into consideration the hypotheses by Monteith (2009) and Histøl & Hjeljord (2013) where the response in the moose population can be delayed, we find that the change in browsing pressure is pointing towards too high numbers of moose in the western range. Combining this with the findings in browsing pressure in the western range from Conradi (2011) and Wam et al. (2010), further reduction in numbers can therefore be necessary to improve body mass.

Concluding remarks

This study, along with earlier studies on browse availability and utilization does not provide a conclusive answer to whether the problem rests with the western moose population as such or lack of browse. We cannot see any effects of the reduced moose population on the carcass weights, and it does not appear to be any drastic differences in browse availability between the ranges. This indicates that it is not the browse availability that limits the western moose population to rebound, although it can be a decline in total browsing area. My results show that browse availability has been better in the west through the last 15 years, and that birch is a much higher proportion of the available browse in the east. Browsing pressure has also been lower in the west, compared to the east. However, over the last 5-7 years, the browsing pressure on younger clearcuts in the west has increased compared to the east. It appears that the conditions for the western moose population have thereby become worse today. Given the results in this and earlier studies, the need for further research should not be focused on browse alone. More research on other influences such as cohort effects, effects of topography and climate, tick-borne diseases, and differences in site quality between the ranges should be conducted. A drastic reduction of the moose population in a trial area could be interesting to see if a very low population would fare better, but since todays sites are less fertile, we could also expect the carcass weights to remain low in the west until the sites logged in the 1950's are logged again. In the future, we should be aware and keep a strict moose population to avoid this situation again.

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