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Distance of Life: Moose Dispersal from Birth to Death

- *Livsdistans: älg spridning från födsel till död*

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Abstract

Moose is the most important big game animal in Sweden, with a great impact on its environment, yet little is known of their movements early in life and therefore we studied a moose population in northern Sweden – their dispersal from birth to death.

We found that mean dispersal distance was 11,5 km \pm 2 km (mean distance in kilometers \pm 95% C.I.) and ranged between 120 meters and 76 km. Males dispersed further than females ($p < 0,0136$), the mean distance for females ($n=70$) was 7,5 km \pm 2,5 km and 14,5 \pm 3,5 km for males ($n=90$). Moreover, dispersal significantly increased with age ($p=0,0001$). We also tested if sex interacted with age as an explaining variable for dispersal but no evidence was found ($p=0,8637$). To evaluate whether these patterns should be considered in the harvest and management of moose, we compared mean moose dispersal distance with the mean size (i.e. radius) of a VVO (hunting area). There was a clear significance that moose dispersed further than the radius of a mean-sized VVO. Our findings show that moose population in northern Sweden is highly dynamic in the sense of their spatial distribution and there're also clear demographical divergences in their dispersal. This is important to both moose managers, who have serious ecological factors to govern and also to moose hunters, who will not shoot their "own" moose. Both factors show the importance of managing moose at the appropriate scale.

Key words: *Alces alces*, forestry, hunter, harvest, management, movement, philopatry, source-sink

Sammanfattning

Älg är det viktigaste jaktbara storviltet i Sverige med stor påverkan på sin omgivning. Trots det vet man inte så mycket om deras rörelsemönster och därför har vi studerat en älgpopulation i norra Sverige – en analys av deras spridning från födsel till död.

Vi såg att medeldistansen var $11,5 \text{ km} \pm 2 \text{ km}$ (medeldistans i kilometer \pm 95% K.I.) med en spridning mellan 120 meter och 7,6 mil. Vi såg också att hanar spred sig längre än honor ($p < 0,0001$) där medeldistansen för honor ($n=70$) var $7,5 \text{ km} \pm 2,5 \text{ km}$ och $14,5 \pm 3,5 \text{ km}$ för hanar ($n=90$). Älgens spridning i relation till dess ålder var signifikant ($p=0,0136$) där distansen ökade med ökande ålder. Vi såg ingen signifikant skillnad då vi testade om kön var en förklarande variabel till åldersrelaterad spridning ($p=0,8637$). För att se om detta påverkar jakten och skötseln av älg jämförde vi viltvårdområdenas (VVO) medelstorlek (radie) med medeldistansen vid spridning för älg där vi såg att älg spred sig signifikant längre än medelradien av ett VVO. Våra resultat indikerar att älgstammarna i norra Sverige är mycket dynamiska med tanke på dess rumsliga fördelning där tydliga demografiska spridningsskillnader kan ses. Detta påverkar såväl älgförvaltare, med många komplexa ekologiska faktorer att ta hänsyn till såväl som jägare, vilka förmodligen inte kommer att skjuta deras "egna" älgar under jakten.

Nyckelord: *Alces alces*, skogsskötsel, jägare, uttag, skötsel, rörelser, filopatri, källa-sänka

Introduction

Few ungulate species on the northern hemisphere has been subject to such intense studies as the moose *Alces alces*, due to their high impact on environment – both ecological and economic. There has been great interest in large-scale studies in the biology- and ecology of moose (see Franzmann and Schwartz 2007, Hjeljord 2008, Danell and Bergström 2010 for examples). Most concerns have been to the dynamic in growth, reproduction and survival rate (Modafferi and Becker 1997, Gaillard *et al.* 1998, Broberg 2004, Sand 2004, Sand and Bergström 2004) and the dispersal and migration (Sweanor and Sandegren 1988, Labonté *et al.* 1998, Baskin *et al.* 2004). The distribution and home range (Cederlund and Sand 1992, 1994) with habitat- and food selection (Cederlund and Okarma 1988, Cederlund and Sand 1992, Ball *et al.* 2001) following life-history patterns and demography (Ericsson 1999, Sand 2004, 2006) as well as philopatry (Ball *et al.* 2001) are examples which have been studied thoroughly.

One subject that has been less studied is the sex-specific patterns of moose dispersal – a topic suggested to be important by Ericsson (1999). The general dispersal of birds and mammals (Greenwood 1980) and of northern deer species have been studied by Robinette (1966), Nelson and Mech (1984) and Hjeljord (2001). Dispersal occurs in many organisms to optimize their fitness and is defined in Begon *et al.* (2006) as “...a spreading of individuals away from others...”, where the driving force may be unknown or vary, but theories point out several possible reasons. For example: to maximize successful breeding, e.g. avoiding harmful inbreeding or to get better access to mates (Greenwood 1980, Shields 1982). Most deer species are promiscuous, with distinct differences in sex and dispersal. Males usually disperse because of intra-specific competition, e.g. mating and competition for resources. Females are more philopatric due to higher costs in breeding and therefore they cannot risk habitat degradation (Robinette 1966, Hjeljord 2001). These different reasons for dispersal will have impacts on moose population dynamics, working as possible drivers to cause source and sink dynamics (Begon *et al.* 2006) with effects on spatial distribution, gene flow and density (Greenwood 1980). A good example from the real moose world is that high density areas (source's) can “feed” adjacent low density areas (sink's) up to 5 km away in the surrounding areas (Labonté *et al.* 1998).

During the last two centuries, small-scale studies have been intensified, which were aimed at testing for climate effects on moose and hunters (Ball *et al.* 1999), moose behavior related to human activity (Neumann 2009, Baskin *et al.* 2004) and moose escape behavior (Baskin *et al.* 2004) as examples – all areas of interest and important to implement when adaptive management goals are set and moose are harvested. Studies on age- and sex-specific patterns of moose mortality in northern Sweden, shows that selective harvest on male moose have had great impact on factors like sex-ratios and age-structures and that prudent management is important to attain a healthy moose population in longer terms (Ericsson 1999, Sylvén 2003) – a collaboration with sage managers, hunters and land owners is needed. Wide eco-biotic effects like these have also been documented by Sylvén (1995, 2003) who have made population models on moose in southern Sweden due to different hunting strategies. Stochastic abiotic environmental factors such as weather are known to be crucial to survival of wild ungulates (Simard *et al.* 2010, Brown 2011). Ball *et al.* (1999) predicted that climate changes may alter patterns of moose mortality, and that human predation (i.e. hunting) is by far the largest cause of mortality in the Swedish moose population (81% of the females and 91% of the males died of a hunters bullet) Ericsson (1999).

However, less effort has been made to analyze dispersal of moose during their whole lifespan, since most of the studies on movements have been made to detect patterns in their adult seasonal migration and philopatry (Sweanor and Sandegren 1988, Ericsson 1999, Ball *et al.* 2001). Another aspect that surprisingly few have been looking at is moose dispersal with respect to forestry, the dominating land-use which is known to alter habitat composition and therefore can cause considerable effects on moose population dynamics (Peek *et al.* 1976). So, what do we know about sexual differences in dispersal of moose today? Well, there are a handful of studies – some contradicting each other. Results from studies of moose-dispersal in North America, made by Gasaway *et al.* 1980 and Labonté *et al.* 1998, showed no sexual difference in dispersal, where Labonté *et al.* also did see great variation between individuals. On the other hand, studies from Sweden (Sweanor and Sandegren 1988, Cederlund and Sand 1992, Cederlund and Sand 1994 and McGuire 2000) showed that males dispersed further – about twice as long as females. Another difference showed up when testing for use of home range size between sexes. Although, the studies from 1988 and 1992 showed positive correlation between age and home range size, the study by Cederlund and Sand (1992), which was done in the southern parts of Sweden at Grimsö, showed that female home ranges correlated positively with their natal area and never overlapped less than 40% whereas males had weaker correlation to their natal area (most in their first year with <40% overlap), resulting in less or no dispersal for females. In the sense of spatial distribution, the result displays that males are likely to disperse longer than females due to their larger home range size – differences that increase with age (Hjeljord 2008). Dispersal initiates when the cow is about to give birth to a new calf, usually when the old calf is one or two year old. Before that, the calf has accompanied its dam during the winter (Franzmann and Schwartz 2007). In this population there are both non-migratory and migratory moose resulting in large difference in movement of individuals (Ball *et al.* 2001).

Moose population dynamics, with spatial- and temporal variation in sex- and age composition (i.e. demography) are important parameters to consider for the management of moose populations. To understand and to scrutinize these processes we have used data from radio-collared moose's to see if there is any divergence in dispersal between the two sexes or/and due to age. If so, we will consider causes and consequences of hunting in general and harvest management in particular. The following hypotheses were set up to answer these questions:

- i. *majority of individuals disperse.* Due to past observations of home-ranges and dispersal of ungulates which reported that dispersal may occur, we want to investigate if moose disperse in our area.
- ii. *dispersal of males are greater than those by females.* Due to the previous observations about sex-specific dispersal, which reported that males usually disperse further, we want to see if distance of males are greater than those achieved by females (male distance > female distance).
- iii. *dispersal increase with age (age-classes 0-3).* Due to past observations on spatial age-distance distribution, which reported that distance and home range size (males) of dispersal increased with age, we expect older moose to disperse further than younger ones (dispersal of age-class; $1 < 2 < 3$).
- iv. *dispersal are greater than hunting areas (VVO's).* By comparing the mean size of a VVO to the distance of moose dispersal, we're able to investigate if hunters are harvesting their "own" moose.

Material and method

Study site

The study area (Figure 1) is located in the coastal parts of Västerbotten County in northern Sweden (64°00' N, 20°45' E) and covers about 100 x 40 km. The landscape is dominated by the coniferous trees norwegian spruce *Picea abies* and scots pine *Pinus sylvestris* and where birch *Betula* spp., aspen *Populus tremula*, willows *Salix* spp. and rowan *Sorbus aucuparia* are the most common deciduous trees. The field layer consists essentially of bilberry *Vaccinium myrtillus*, lingonberry *Vaccinium vitis-idaea*, crowberry *Empetrum nigrum* and heather *Calluna vulgaris* (see Ball *et al.* 2001 for further details of the study area).

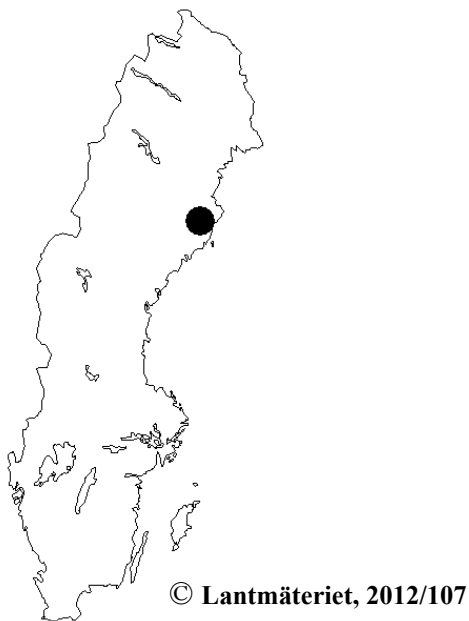


Figure 1. Map of Sweden showing the study area (black dot) at the coastal parts of Västerbotten.

Figur 1. Karta över Sverige med studieområdet (svart punkt) vid Västerbottenskusten.

Data collection

From 1995 to 2001, adult female moose were immobilized from helicopter with a dart gun for radio-collar attachment. Every third day during calving time, mainly between the last days in May and the first week in June (Hjeljord 2008), these were located with a hand-held radio receiver to determine if calving had taken place. If so, the calves were ear-tagged and their position recorded using hand-held GPS receiver (WGS 84) and in some cases equipped with a radio-collar. Position was also documented for their site of death when shot by hunters during the hunt between September and December (Ericsson 1999, Ball *et al.* 1999). Hunting team areas, in Sweden known as “viltvårdsområden”, (hereafter called VVOs) from twelve coastal

hunting districts ($N=581$) in Västerbotten (see Table 1 in Appendix 1) were collected from The administer Board of Västerbotten (Länsstyrelsen 2012).

Moose age classification

Moose lifespan were classified into 4 groups (0-3), hereafter called calves (0); yearlings (1); sub-adults (2) and adults (3) – ranging from 0-1 years old (calves), $n=76$ (47,5%); 1-2 years old (yearlings), $n=30$ (19%); 2-3 years old (sub-adults), $n=24$ (15%); >3 years old (adults), $n=30$ (19%). Maximal age of an individual was 6 years old in our sample.

Analysis

Statistical analysis were performed in JMP 9.0.0 (SAS Institute 2010) and OriginPro (Microcal 2011). To test if there are any correlation between the parameters sex and age, with distance as an response variable, we performed an analyze of variance (i.e. ANOVA) to compare mean values. The raw data did not satisfy the assumption of uniform residual variance, so the data was log-transformed (Kozak *et al.* 2007). ArcMap 10 (ESRI 2010) was used to calculate distance (analysis tool; point distance) of dispersal which we double checked by manually selecting moose object number with the measure tool. To see whether the size of the VVO's differs from distance of moose dispersal, a Student's Two-sampled t-test was done. To enable this, we assumed VVO-shapes to be circular which enabled us to make distance comparisons of moose distance and radius of the VVO's. Note, this method will show the minimum radius of the VVO whereas the actual VVO are irregularly shaped and will always be greater.

Results

Distance

Mean distance (observed values) for both sexes ($N=160$) was $11,5 \text{ km} \pm 2 \text{ km}$ (mean distance in kilometers \pm 95% C.I.), ranging between 120 meter (min.) and 76 km (max.). Mean distance for females ($n=70$) was $7,5 \text{ km} \pm 2,5 \text{ km}$ and $14,5 \pm 3,5 \text{ km}$ for males ($n=90$), nearly twice the distance of females (Table 1). Notable was that both min. (120 meter)- and max. (77 km)- distances were done by males, where the minimum traveler was two years old and the maximum traveler was a yearling. Thus, there seems to be great variations in dispersal distances.

Table 1. Moose mean-distances (km) with 95% C.I., for each sex and divided into age-classes (0-3, with sample size n_i) where calves=0; yearlings=1; sub-adults=2; adults=3. The analysis was executed in JMP. Highlighted numbers are mean-distance asymptotes.

Tabell 1. Medeldistans för älg (km) med 95% K.I. för båda könen och uppdelat i åldersklasser (0-3, med provstorlek n_i) där calvar=0; fjolårskalvar=1; sub-adulta=2; adulta=3. Analysen var utförd i JMP. Fetmarkerade siffror är asymptoter för medeldistans.

Age-class	Females ($n=70$)					Males ($n=90$)				
	0 ($n=38$)	1 ($n=14$)	2 ($n=8$)	3 ($n=10$)	All age-classes ($n=70$)	0 ($n=38$)	1 ($n=16$)	2 ($n=16$)	3 ($n=20$)	All age-classes ($n=90$)
Mean dist. \pm 95% C.I.	2,9 \pm 0,8	13,8 \pm 10	14,6 \pm 12,7	11,6 \pm 8,3	7,5 \pm 2,5	8 \pm 4,7	12,5 \pm 6,7	26,5 \pm 7,9	19 \pm 7,5	14,5 \pm 3,5

Differences in distance

We tested if there are any relationship between distance, age and sex with an ANOVA test. Three different parameters were used: (1) sex, (2) age-class and (3) the sex*age-class interaction. (1) The difference in distance between sexes was highly significant ($p<0,0136$). (2) The difference are also significant ($p<0,0001$) in the correlation between distance and age. (3) Our analysis did not reveal any significant interaction ($p=0,8637$) in distance by sex and age-classes, i.e. sex and age-class have no effect on each other (Table 2).

Table 2. Results from the ANOVA using distance as an response variable and sex, age-class and sex*age-class used as parameters. F-value shows how much of the variation in the response variable that are explained by an specific parameter (increasing F-value increases the explanatory power of the parameter). Significant p-values are highlighted.

Tabell 2. Resultat från ANOVA med distans som responsvariabel samt kön, åldersklass och kön*åldersklass som parametrar. F-värdet visar hur mycket av variationen i responsvariabeln som förklaras av en specifik parameter (ju större F-värde för en parameter desto starkare förklaringsvärde har den). Signifikanta p-värden är fetmarkerade.

Response variable	Parameter	F-value	P-value
	Sex	6	<0,0136
Distance	Age-class	20	0,0001
	Sex*Age-class	0,2	0,8637

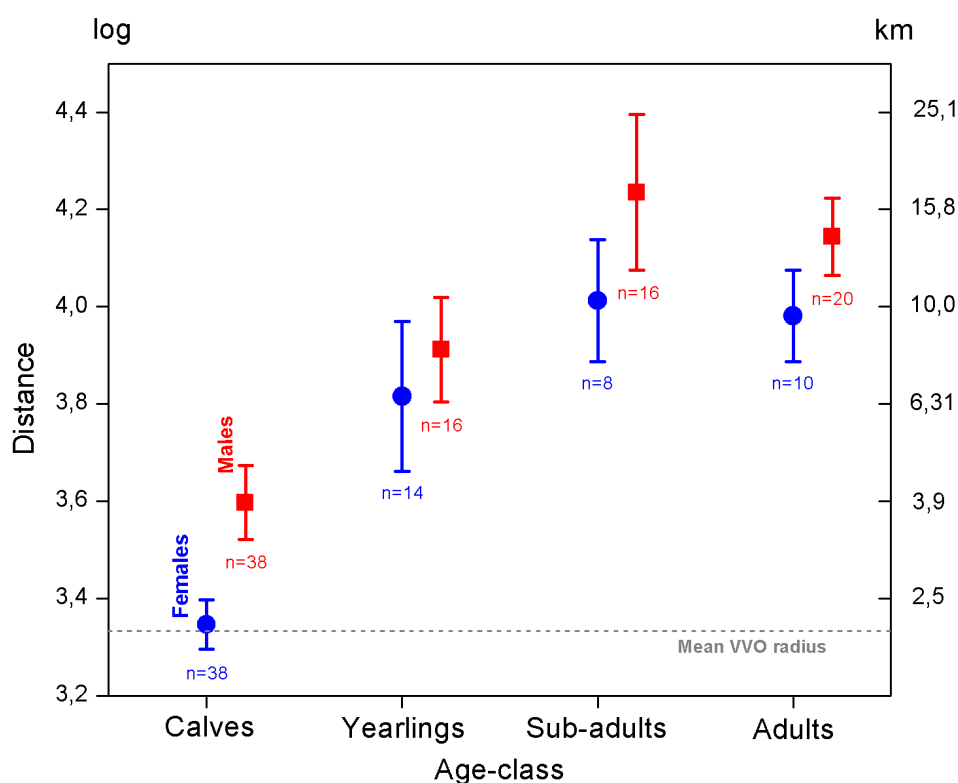


Figure 2. Distance (means \pm standard errors in log-transformed values and in kilometers) of moose ($n_{\text{females}}=70$; $n_{\text{males}}=90$; $N=160$) dispersal between sexes (blue plots=females; red plots=males) and age-classes, divided into four age-classes (calves, yearlings, sub-adults and adults). Mean value of hunting team area (VVO)-radius ($n=581$) are shown as a gray dotted line. See Table 2 for p-values.

Figur 2. Distans (medel \pm standardfel i logtransformerade värden och i kilometer) för spridning av älg ($n_{\text{hanor}}=70$; $n_{\text{hanar}}=90$; $N=160$) uppdelade av kön (blåa punkter=hanar; röda punkter=hanor och åldersklasser uppdelade i 4 åldersklasser (kalvar, fjolingar, sub-adulta och adulta). Viltvårdsområdenas ($n=581$) medelradie visas som en prickad grå linje. Se Tabell 2 för p-värden.

VVO radius vs. moose distance

We looked at the distribution of the mean-radius of VVO's ($n=581$) and distance of moose dispersal (both sexes). There was significant difference between the two mean values ($p<0,001$; Two-sample t-test) where mean distance of dispersal was $11,5 \text{ km} \pm 2 \text{ km}$ meter and where mean radius of the VVO's were $2 \text{ km} \pm 75$ meter. There was also a highly significance in the difference of the mean values when looking at the two sexes (both with $p<0,001$; Two-sample t-test) where mean distance for female was $7,5 \text{ km} \pm 2,5 \text{ km}$ and where males mean value was $14,5 \text{ km} \pm 3,5 \text{ km}$ (Table 3).

Table 3. Comparison of moose dispersal distance (means \pm 95% C.I.) of both sexes vs. hunting team area (VVO) radius. VVO areas were transformed into circles to make comparisons possible. All p-values are significant.

Tabell 3. Jämförelse av älgens spridningsdistans (medel \pm 95% K.I.) av båda könen samt radien för viltvårdsområden (VVO). Areor för VVO:na gjordes cirkulära för att möjliggöra jämförelser. Alla p-värden är signifikanta.

	Mean distance \pm 95% C.I.	P-value
Both sexes ($N=160$)	$11,5 \pm 2,2$	$<0,001$
Female ($n=70$)	$7,5 \pm 2,5$	$<0,001$
Male ($n=90$)	$14,5 \pm 3,5$	$<0,001$
VVO ($N=581$)	$2 \pm 0,076$	

Discussion

We found that the mean distance was 11,5 km (sexes combined), ranging between 120 meter and 76 km – which is quite a variation. This variation was greater within males than females. If we look at an study done by McGuire in 2000, who (partly) looked at moose home range size in our area, we can see that distance done by moose – of both sexes at all age-classes (see Table 1) – are greater than mean home range size calculated by McGuire. Therefore, we suggests that dispersal occurs, which also are found in several studies, for examples, see Robinette (1966), Nelson and Mech (1984) and Hjeljord (2001). Compared to the study from Grimsö in southern Sweden, by Cederlund and Sand in 1992, our distances of dispersals were greater, though similar patterns were seen (e.g. temporal-, and to a certain degree spatial patterns of spread) whereas they did not confirm the prediction of uniform dispersal (Robinette 1966, Nelson and Mech 1984 and Hjeljord 2001). These differences may be a result of a north-south gradient – perhaps suggesting that home-range size increases with increased latitude (Franzmann and Schwartz 2007). One contributing factor to the great variance in dispersal could be due to the large time-frame data was sampled, ranging from September to December. The data might include some animals who had migrated to their winter range before the end of the hunting season, although in most years this number would be small (Ball *et al.* 1999).

Looking at sex-specific patterns in deer species, in many cases males disperse further than females (Sweonor and Sandegren 1988, Cederlund and Sand 1992, Cederlund and Sand 1994, McGuire 2000). When we tested for divergence in dispersal distances between sexes, our results showed clear evidence ($p=0,0136$) in agreement with previous observations that males dispersed farther than females (Table 2 and Figure 2), which Cederlund and Sand also saw in their study as well as Sweonor and Sandegren – both studies from southern Sweden. Research from North America (Gasaway 1980, Labonté *et al.* 1998) had contradictory results though: no significant difference in length of dispersal between sexes. Although this isn't shocking! Overall, the moose population density is far higher in Sweden. Pellet sampling surveys showed populations in our area of around 0,8 moose/km² (Ericsson 1999), more than three times as dense as the moose population that Labonté *et al.* studied in Canada (0,03-0,32 moose/km²). Both areas have also had high hunting pressure (e.g. favoring males for trophies), a factor that can alter the demography (e.g. calf sex-ratio) and life history of moose (Broberg 2004). Altogether, we would be surprised if no divergence were exhibited between the two continents due to differences in life-history. Our study also indicates that male calves dispersed further than female calves (Table 1 and Figure 2) even during the first year. It is known that almost all calves will follow their mother of their first year in life (Franzmann and Schwartz 2007), so we suggest that female moose rearing male calves may demand larger home range areas than dams rearing female calves and that further study is needed.

We found strong evidence that dispersal increases with age ($p<0,0001$) which lead us to wonder why that is (Table 2). Does it depend on the fact that the calf stays with its mother during their first year in life, resulting in short distances in dispersal during that first year (Franzmann and Schwartz 2007, Broberg 2004)? Other moose studies have documented that during the second year in life (as a yearling), most of them separate from their mother in early summer, between 7-29th of May (Cederlund *et al.* 1987, Ballard *et al.* 1991). Studies by Cederlund *et al.* in Sweden (1987) and Cederlund and Sand (1992) showed that dispersal increased the first month after calf separation from its mother (Cederlund *et al.* 1987). Studies from North America show that moose will establish their own home range at the time of their third year (Franzmann and Schwartz 2007) and that home range size of the offspring

positively correlates to their mother's home range size (Ballard *et al.* 1991). According to this knowledge and to our data, saying that dispersal may decline a bit at upper ages (Table 1), we think that a possible explanation for decreasing dispersal by adults are an effect of their increasing home range size (Cederlund and Sand 1994). For example: As long as they are young and having no home range of their own, distance of dispersal will increase (at least for most of them) when "searching" for one. As soon as they find their home range, there's no need to disperse any more and length of dispersal will stabilize – or even decrease (Cederlund *et al.* 1987). Why might there be a decrease in dispersal at the upper ages we studied? If we suppose their home range to be circular and that they will (can) spread at any (all) directions, we shouldn't see a decrease in dispersal. Still, home range shape and dispersal length may vary a lot in reality as a consequence of unknown biological reasons, and we suggest that this is an area that needs to be further investigated. At this stage, due to the larger home range size, we think it's possible that they're closer to their native area (place of birth) which is a factor that may influence our analysis of dispersal.

So far, our results showed clear evidence that dispersal occurs – in both sexes and at all ages (Table 1 and Figure 2). Therefore, we wanted to see if age and sex interacted with distance of dispersal. The result from the ANOVA (Table 2 and Figure 2) showed no evidence of an interaction between sex and age. Maybe that's not so strange though, saying both sexes having the same capability to disperse independent of their age. The dispersal pattern shown by our moose made us curious as to whether hunting team areas, VVO's, are harvesting their "own" moose or not, a parameter of interest for both hunters and managers. Our results suggest that hunting teams may often not shoot their own moose: $\text{radius}_{\text{VVO}} < \text{dispersal}_{\text{moose}}$ (Figure 2). The mean radius of a VVO was 2 km \pm 75 meter whereas mean distance of dispersal was 11,5 km \pm 2,2 km ($p < 0,001$). Looking at the two sexes separately, we observed the same high significance ($p < 0,001$). Does this mean that hunters don't shoot their "own" moose? Well, at a small scale – from the hunters (VVO-) view – the dispersal is still highly diverse in distance, differing among VVO's with a heterogeneous moose population structure where some individuals don't disperse whereas other do. Due to shorter distance of dispersal (Table 2 and Figure 2) our data suggest that it is more likely that females are born and shot at the VVO where they were born. At a larger scale – the managers view – the nature of the habitat (i.e. much variation in habitat quality at the large scale, causing more or less food abundance) may contribute to distance in dispersal more than density dependent- and mating factors (Franzmann and Schwartz 2007), but the opposite has also been showed in other studies (Hjeljord 2001).

To summarize, we found that moose in our area are likely to disperse, in both sexes and at all ages (Table 1 and Figure 2). We also found that males dispersed further than females and that males had greater variation (Table 1 and Figure 2), the same patterns that were seen in the studies by Sweanor and Sandegren (1988), Cederlund and Sand (1992) and McGuire 2000. However, other studies did not document the same clear relationship between sex and distance, only detecting dispersal by males due to the highly philopatric females (Cederlund and Sand, 1994) or no difference at all (Gasaway 1980, Labonté *et al.* 1998). Still, we know that moose harvest have great impact on moose population dynamics, such as sex-ratio (often biased for females due to selective hunting on males), demography (i.e. altering age-structure, e.g. younger- and less dominant males), genetics (i.e. lack of genes from dominant males) and in their rate of increase causing both spatial- and temporal variation in moose population density. Dispersal is therefore a parameter to consider due to its large effects on the yield in a given locality. Why do hunters care if there're shooting their "own" moose? Well, probably few will put in a large effort to enhance the wildlife if they feel that somebody else will take

the benefit of any extra moose. It is clear that moose management has to be seen at a large scale, where several VVO's have to collaborate and where hunters will gain the reward of their work. In January 2012, a new adaptive moose management was set up – a system which takes more consideration of both hunters and land-owners by giving them substantial participation – which is necessary to gain acceptance between interests and to get a sustainable harvest over time (Danell and Bergström 2010). Here, several VVO's are merged into "älgförvaltningsområden" (ÄFO's) ranging between 50 000 - 80 000 ha (12,6-16 km radius) from south to north, taking greater considerations of moose spatial distribution in order to manage their own moose population (Öhman *et al.* 2011) containing at least 80% of the population (Sandström 2011). By comparing the ÄFO radius with mean distance of dispersal ($11,5 \pm 2,2$ km) it seems possible that an ÄFO is containing at least 80% of the population. Adaptive management relies on adequate data (Danell and Bergström 2010), both from surveys and from research and more knowledge is needed to get deeper insights in the dispersal of moose individuals and on moose population dynamics – effects strongly influenced by land-use like forestry and agriculture.

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References

- Ball, J.P., Nordengren, C. and Wallin, K. 2001. *Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden*. *Wildl. Biol.* 7:39-47.
- Ball, J. P., Ericsson, G. and Wallin, K. *Climate changes, moose and their human predators*. 1999. *Ecol. Bull.* 47:178-187.
- Ballard, W. B., Whitman, J. S. and Reed, D. J. 1991. *Population dynamics in south-central Alaska*. *Wildl. Monogr.* 114, 1-49.
- Baskin, L., Ball, J. P. and Danell, K. 2004. *Moose escape behavior in areas of high hunting pressure*. *Alces*. Vol. 40: 123-131.
- Begon, M., Townsend, C. R., and Harper, J. L. 2006. *Ecology – from individuals to ecosystems*. 4th ed. Blackwell Publishin Ltd. Utopia Press.
- Broberg, M. 2004. *Reproduction in moose – Consequences and conflicts in timing of birth*. Department of Applied Environmental Science, Göteborg University.
- Brown, G. S. 2011. *Patterns and causes of demographic variation in a harvested moose population: Evidence for the effects of climate and density-dependent drivers*. *Journal of Animal Ecology*. Vol 80 (6) pp. 1288-1298.
- Cederlund, G. N., and Okarma, H. 1998. *Home range and habitat use of adult female moose*. *J. Wildl. Manage.* 52 (2): 336-343.
- Cederlund, G. N., Sandegren, F. and Larsson, K. 1987. *Summer movement of female moose and dispersal of their offspring*. *J. Wildl. Manage.* 51 (2): 342-352.
- Cederlund, G. N. and Sand, H. K. G. 1992. *Dispersal of sub-adult moose (*Alces alces*) in a non-migratory population*. *Can. J. Zool.* 70: 1309-1314.
- Cederlund, G. N. and Sand, H. K. G. 1994. *Home range size in relation to age and sex in moose*. *J. Mamm.* Vol. 75 (4): 1005-1012.
- Danell, K., Bergström, R. (red.). 2010. *Viltet, människa, samhälle*. Repro, Stockholm.
- Ericsson, G. 1999. *Demographic and life history consequences of harvest in a Swedish moose population*. Doctoral thesis. Swedish University of Agricultural Sciences, Umeå.
- ESRI. 2010. *ArcMap 10.0*. Environmental System Research Institute, Inc., Redland, C.A., USA.
- Franzmann, A. W., Schwartz, C. C., McCabe, R. E. 2007. *Ecology and management of the North American moose*. 2nd ed. University press of Colorado, Boulder.
- Gaillard, J. M., Festa-Bianchet, M. and Yoccoz, N. G. 1998. *Population dynamics of large herbivores: variable recruitment with constant adult survival*. *TREE*. Vol. 13. No. 2. pp. 58-63.

- Greenwood, P. J. 1980. *Mating systems, philopatry and dispersal in birds and mammals*. Anim. Behav. 28: 1140-1162.
- Hjeljord, O. 2008. *Viltet – biologi og forvaltning*. Tun förlag, Oslo.
- Hjeljord, O. 2001. *Dispersal and migration in Northern forest deer – are there unifying concepts?* Alces. Vol. 37 (2): 353-370.
- Kozak, A., Kozak, R. A., Studhammer, C. L. and Watts, S. B. 2007. *Introductory Probability & Statistics – Applications for Forestry & the Natural Sciences*. Wallingford: CAB International.
- Labonté, J., Oullet, J-P., Réhaume, C. and Bélisle, F. 1998. *Moose Dispersal and Its Role in the Maintenance of Harvested Populations*. J. Wildl. Manage. Vol. 62., No. 1: 225-235.
- Länsstyrelsen. 2011. *Älgtilldelning A-licensområden 2011*. [Online] Tillgänglig: <http://www.lansstyrelsen.se/vasterbotten/SiteCollectionDocuments/Sv/djur-och-natur/jakt-och-vilt/%C3%84lgjakt/Tilldelning/Tilldelningslista%202011.xls> [2012-03-29]
- McGuire, R. L. 2000. *Dispersal and the inheritance of spatial and temporal movement patterns in moose: Following in mother's footsteps?* Examensarbete i ämnet zoökologi. Institutionen för skoglig zoökologi, SLU, Umeå.
- Microcal Software, Inc. 2011. *OriginPro 8.6*. One Roundhouse Plaza. Northampton, MA01060 USA.
- Modafferi, R. D. and Becker, E. F. 1997. *Survival of radiocollared adult moose in Lower Sustina River Valley, south central Alaska*. The Journal of Wildlife Management, Vol. 61., No. 2., pp. 540-549.
- Nelson, M. E. and Mech, L. D. 1984. *Home-range formation and dispersal of deer in North eastern Minnesota*. J. Mamm., 65 (4): 567-575.
- Peek, J. M., Urich, D. L. and Mackie, R. J. 1976. *Moose habitat selection and relationships to forest management in northeastern Minnesota*. Wildlife Monographs. No 48: 3-65.
- Robinette, W. L. 1966. *Mule Deer Home Range and Dispersal in Utah*. J. Wildl. Manage. Vol. 30., No. 2335-349.
- Sand, H. 2004. *Reproduktion hos älgkor*. Skogsvilt III, Vilt och landskap I förändring. Grimsö forskningsstation, SLU. pp. 118-122.
- Sand, H. and Bergström, R. 2004. *Reproduktion hos älgar – smakar det så kostar det*. Skogsvilt III, Vilt och landskap I förändring. Grimsö forskningsstation, SLU. pp. 123-128.
- Sand, H. 2006. *Life history in female moose (Alces alces): The relationship between age, body size, fecundity and environmental conditions*. Oecologia. 106, iss. 2: 212-220.
- Sandström, C. 2011. *Adaptiv älgförvaltning nr 13: Det organisatoriska ramverket*. FaktaSkog Nr. 22. Sveriges Lantbruksuniversitet, Umeå.
- SAS Institute Inc. 2010. *Using JMP 9*. Cary, NC: SAS Institute Inc.

- Shields, W. M. 1982. *Philopatry, inbreeding and the evolution of sex*. State university of New York Press, Albany.
- Simard, M. A, Coulson, T., Gingras, A. and Côté, S. D. 2010. *Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions*. Journal of Wildlife Management. Vol. 74 (8) pp. 1671-1685.
- Sweaner, P. Y & Sandegren, F. 1988. *Migratory behavior of related moose*. Holarct. Ecol. 11:190-193.
- Sylvén, S. 1995. *Moose harvest strategy to maximize yield value for multiple goal management – a simulation study*. Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala. Agricultural systems. 49: 277-298.
- Sylvén, S. 2003. *Management and regulated harvest of moose (Alces alces) in Sweden*. Department of Conservation Biology, Swedish University of Agricultural Sciences.
- Öhman, K., Edenius, L. and Holmström, H. 2011. *Adaptiv Älgförvaltning nr 11: Den svenska älgstammens förvaltning och foderprognoser*. Sveriges Lantbruksuniversitet, Umeå.

Appendix 1

Table 1. List of the twelve hunting districts with the hunting team areas (VVO's) that were used, located in the coastal area of Västerbotten (Länsstyrelsen 2012).

Tabell 1. Lista med de tolv jaktströmmarna med viltvårdsområden (VVO:n) från Västerbottenskusten som användes i studien (Länsstyrelsen 2012).

Hunting districts	Sample size of VVO's
Nordmaling	56
Bjurholm	43
Vindeln	79
Robertsfors	58
Nysätra	18
Vännäs	40
Umeå	76
Sävar	44
Holmön	1
Skellefteå	24
Lövånger	39
Burträsk	103
N_{tot}	581