

WOLF PREDATION ON MOOSE - A CASE STUDY USING HUNTER OBSERVATIONS

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ABSTRACT: We studied predation by colonizing wolves on a high density and highly productive moose (*Alces alces*) population in south-eastern Norway (about 1.5 moose and 0.01 wolves per km² in winter). As indices to population changes, we used hunter observations. Over the summer, the wolf pack utilized about one tenth of their total territory (530 km²), with the den area as the centre of activity. Of the main prey taken (moose, roe deer, and beaver), moose calves contributed 61% of the biomass ingested by wolves in summer. Hunting statistics and hunters' observations of moose showed no changes for the territory as a whole after wolves settled there in 1998. However, in the den areas (60 - 80 km²) the number of calves per cow and the total number of moose seen per hunter-day significantly decreased during the year of wolf reproduction. The following year, though, both indices increased again. We speculate that some of the lack of overall effects might be due to increased fecundity in cows that lost their calf. As the wolves changed their den from year to year, den areas were spatially spread over time. The pressure from wolf predation will differ between cohorts in the same area, and landowners should adjust their hunting quotas accordingly.

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The return of wolves (*Canis lupus*) to southern Scandinavia introduces several problems to wildlife management. One is a predicted reduction in harvest of moose (*Alces alces*) due to wolf predation. To ease the resistance among Norwegian moose hunters, the Directorate for Nature Management is evaluating the possibility of reimbursing landowners yearly losses of moose to wolves. Due to the highly dynamic nature of the predator - prey relationship between wolves and moose (Messier 1994, Ballard and Van Ballenberghe 1998, Hayes and Harestad 2000), an eventual reimbursement plan requires that the effects of predation are estimated locally.

In this study we investigate the influence of wolf predation on a high-density, productive moose population in south-eastern Norway. We expect wolf predation to have a relatively small effect on this popu-

lation, compared to less dense moose populations with lower recruitment rates (Andr en et al. 1999). However, within a wolf territory, we also expect predation to vary locally. Since the den with rendezvous sites is the centre of activity throughout the summer (Mech 1970), we expect predation losses to be higher among moose living close to the den. Hence, landowners in the neighbourhood of the den may suffer a higher loss of moose to wolves than will landowners in other parts of the territory.

How landowners should adjust their hunting quotas to mitigate the effects of predation depends not only on the number of moose taken, but also on which sex- and age-group is preyed upon. As there are few old individuals among Scandinavian moose, we expect the wolves to prey particularly on calves (Fritts and Mech 1981, Boyd et al. 1994, Olsson et al. 1997). However, when

nursing calves are killed by brown bears (*Ursus arctos*), there appears to be an increase in the fecundity of the cow the next year (Swenson et al. 2001). A compensation effect may also apply to wolf predation on moose.

In Norway, moose populations are monitored routinely by a system in which hunters report on moose seen during the hunting season. Because of large confidence limits, the hunter observation indices are not suitable for predicting absolute values of population size and recruitment rate. However, they appear well suited to predict directional changes (Fryxell et al. 1988, Solberg and Sæther 1999).

In this study we use hunter observation indices to look for changes in the moose population at two different scales: (1) within the wolf territory as a whole; and (2) within the wolves' den areas.

STUDY AREA

The study area is located in south-eastern Norway (59°33'N, 11°02'E), about 30 km east of the Oslo fjord. Most of the area is forested, and part of the boreonemoral zone, with spruce (*Picea abies*) and pine (*Pinus silvestris*) being the dominant tree species. Lakes cover < 0.5% of the area, and bogs are infrequent. Mature forest is harvested by clearcutting, and birch (*Betula pubescens* and *B. pendula*) and rowan (*Sorbus aucuparia*) dominate on clearcuts soon after logging. Clearcuts are small and usually < 10 ha. Elevations range from 40 to 260 m and the topography is broken by small creek valleys. The ground is usually snow-covered from December to April, with an average snow depth of 20 cm.

The study area lies within the most high-yielding populations of both moose and roe deer (*Capreolus capreolus*) in Norway (Bjar and Selås 1987, Hjeljord and Histøl 1999). There has been no census of the ungulate density, but yearly harvest may

be used as an indication. During 1995-2000 with an apparently stable population of the two species, an average of 0.6 moose and 1.6 roe deer were shot per km² each year. Assuming a yearly finite rate of increase of 1.35 for moose (Hjeljord, unpublished data) and 1.4 for roe deer (Strandegaard 1974), the density may be estimated at 1.5 moose/km² and 4.0 roe deer/km². It is likely that the density of roe deer is actually higher as not all roe deer shot are reported by hunters.

Wolves had been absent from this area for 150 years when a female wolf settled there in 1998. A male wolf joined her shortly after, and a pack was formed. Thereafter the wolf density varied with an average of 0.009 wolves per km² in the winter (for further details see Table 1).

METHODS

Wolf use of the area was investigated by following the radio-collared alpha male from May 1999 to November 2001. The male was located every 30 minutes over a continuous 10-day period. Ten such 10-day periods of intensive triangulation were spread over the year to get a picture of territory use throughout the different sea-

Table 1. Development of a re-establishing wolf pack in south-central Norway 1998-2002 (based on snow tracking and sightings at rendezvous sites). Territory size was 530 km², and there were no bordering packs. (a = adult wolves, j = juvenile wolves, and p = pups.)

	In February	In August
1998	No wolves	1a
1999	2a	2a, 5p
2000	2a, 3j	3a, 4 or 5p
2001	3a, 2j	3a, 8p
2002	1, 2a ¹ , 5 or 6j	No denning
98-02	0.009/km ²	0.017/km ²

¹ no alpha male.

sons.

Wolf summer diet was investigated by analysing faeces collected at the den site in the second week of August, 2000. Scats were analysed for prey remains like claws, teeth, bones, and hair using standard methods as described in Ballard et al. (1987). Samples of hair that we macroscopically judged to belong to different species were later identified microscopically. In some samples it was necessary to study a gelatine casting of the cuticula (Teerink 1991). Blind tests were conducted to check the reliability of the method. We calculated the prey proportions of wolf diet both by occurrence and by biomass (as defined in Floyd et al. 1978). For the latter, we used the equation of Weaver (1993), $Y = 0.439 + 0.008X$, where Y is kg biomass consumed per scat of a particular prey of live biomass X kg. For estimates of biomass of the different prey species, we used the figures given in a Scandinavian study by Olsson et al. (1997).

To investigate the effect of wolf predation on moose population size and reproduction, we used hunting statistics (Central Bureau of Statistics 1995 - 2001), and hunter observations recorded mainly during the first week of the moose hunting season in early October. The hunt on each unit of land is done by a team of moose hunters, and the leader of each team completes the observation forms.

As an indication of moose population size and recruitment rate/fecundity, we used the number of moose observed per hunter-day (8h), and the number of calves per cow (hereafter the c.c. ratio), respectively. We also used the number of calves per cow-with-calf to verify our data, since wolf winter predation in this initial phase of recolonization may have affected the number of maiden cows (so far there have been more female than male moose > 1 year of age killed by wolves in Scandinavia, Sand et al. 2002).

In the statistical analysis we used the 3-year average 1995 - 1997 for each hunting unit as reference data against which we tested changes within the same hunting unit after the wolves settled. The year when the wolf arrived (1998) was not included in the analyses. The territory comprised a total of 19 hunting units, and the den areas 3 - 4 hunting units each. Due to the small number of replicates in the den areas, we grouped all 3 den areas when looking for changes here. On average, there were 37 ± 5.7 SE moose seen within each hunting unit, of which 17 ± 2.4 SE were cows. Our data were normally distributed, and we used paired *t*-tests for all comparisons.

We also compared the moose population within the wolf territory with the moose population in a control area bordering the wolf territory. Initial tests showed that prior to 1998, hunter statistics and observations within the wolf territory were correlated with that of the control area.

RESULTS

Summer Diet

Moose, roe deer, and beaver (*Castor fiber*) (later called main prey species) dominated the prey remains in the collected scats ($n = 151$), contributing 94% by occurrence. Mountain hare (*Lepus timidus*), birds, domestic animals, and unidentified food items contributed the remaining 6%. Moose dominated among the main prey species, contributing 44% by occurrence of main prey. Moose calves appear to be an important part of wolf diet in the study area over the summer, as they made up 95% of all the moose (i.e., 42% by occurrence of main prey). Roe deer contributed 36%, and beaver the remaining 20% by occurrence. For the proportions of biomass ingested see Fig. 1. When we estimated the biomass of main prey species, we did not include 12% prey remains from scats where we could not distinguish juvenile roe deer from juve-

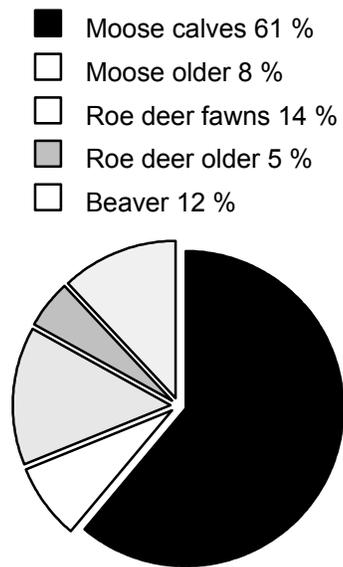


Fig. 1. Consumed biomass of main prey for wolves in south-central Norway based on scat analysis ($n = 151$) collected at the den in August 2000. Adjusted after Weaver (1993).

nile moose.

Summer Territory Use

From April 2000 to November 2001 we recorded 2,961 positions of the radio-collared male, and estimated annual territory size to be 530 km². While the animal regularly used the entire territory during fall/winter, the spring/summer use was more restricted and apparently depended on location of the den. During the summer of 2000 (May - August) more than 90% of the locations we obtained during our 10-day triangulation periods lay within 4 km of the den. The area of primary occupancy extended over approximately 50 km² (Fig. 2), less than one tenth of the total territory. In 2001 the wolves moved their den site 17 km to the south, and our radio-locations indicated a similarly restricted range use during summer (approximately 70 km²). In 1999, the first year when wolves reproduced in the area, no animal was radio-collared. However, sightings of pups, and systematic

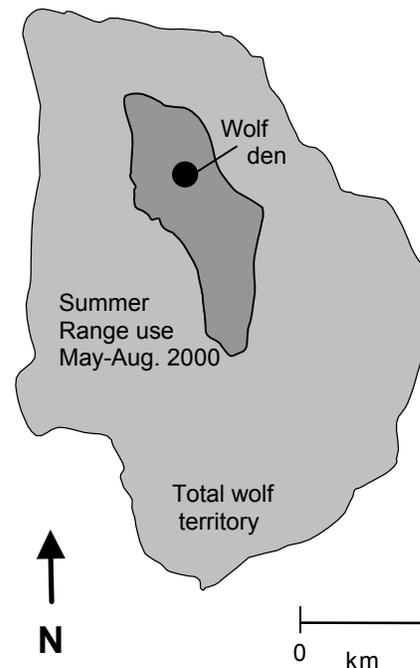


Fig. 2. Den site, summer range and total territory size as determined by triangulation of a radio-collared alpha male wolf in south-central Norway, 2000.

searches for faeces and prey remains, made it possible to locate the den site.

Based on these data we outlined an area of hunting units close to each of the 3 dens where we expected the predation pressure on moose calves to have been most severe. This area, later called the den area, consisted of 4 units around the 1999 den (80 km²), 4 units around the 2000 den, (60 km²), and 3 units around the 2001 den (80 km²). The larger sizes of the 1999 and 2001 den areas are due to both the variable size of individual hunting units and our impression of the area used by the wolves in these two years.

Hunter Observations in the Territory and Control Area

Hunter-observations and harvest data of moose showed few changes in the territory as a whole following wolf colonization in 1998 (Fig. 3). There was neither any

change in the number of moose seen per hunter-day (mean = 0.58 ± 0.08 SE without wolves and 0.60 ± 0.06 with wolves) ($t = -0.28$, 18 df, $P = 0.39$), nor in the total number of moose shot (108 without wolves and 112 with wolves) ($t = -0.62$, 18 df, $P = 0.22$) (Fig. 3). Harvest of calves also remained stable (28 without wolves and 27 with wolves), while the number of yearlings harvested slightly decreased, although not significantly (46 versus 43) ($t = 0.17$, 18 df, $P = 0.47$).

During the study period the hunting quotas were reduced by 7%, while the fulfilment of them increased from 87 to 97%. The total number of days (8 hours) hunted within the territory decreased from 1,649 (1995-1997) to 1,491 (1999-2001). Hence, the hunters apparently had no problem getting all the moose on their quotas.

For the territory as a whole there was no decrease in the c.c. ratio after wolves settled in the area (0.74 ± 0.03 without wolves and 0.74 ± 0.04 with wolves) ($t = -0.01$, 18 df, $P = 0.50$). If we look only at the cows with calves, there was a slight but insignificant increase (1.31 ± 0.04 without wolves and 1.39 ± 0.04 with wolves) ($t = -1.23$, 18 df, $P = 0.11$).

In the control area, the same numbers of moose were hunted in the years 1995-1997 and 1999-2001 (131 vs. 129). There was a small increase in the number of moose seen per hunter-day (from 0.47 ± 0.03 to 0.57 ± 0.09) ($t = -1.86$, 5 df, $P = 0.06$), and there was no change either in the c.c. ratio (from 0.89 ± 0.01 to 0.88 ± 0.02) ($t = 0.29$, 5 df, $P = 0.39$) nor in the number of calves per cow-with-calves (1.32 ± 0.03 vs. 1.34 ± 0.00) ($t = -0.19$, 5 df, $P = 0.43$).

Hunter Observations in the Den Areas

Within the den areas, there were more obvious changes in the hunter observations of moose than for the territory as a whole (Fig. 4). In the years of wolf denning, there was an insignificant decrease in the number of moose seen per hunter-day from what it had been before wolves re-established (from 0.50 ± 0.05 without wolves to 0.45 ± 0.02 in the year of denning) ($t = 0.72$, 10 df, $P = 0.24$). The year following active denning, there were more moose seen within the den areas than before wolves re-established (0.66 ± 0.17), although due to high variance this was not significant ($t = -1.51$, 10 df, $P = 0.08$).

Compared to 1995-1997, the c.c. ratio

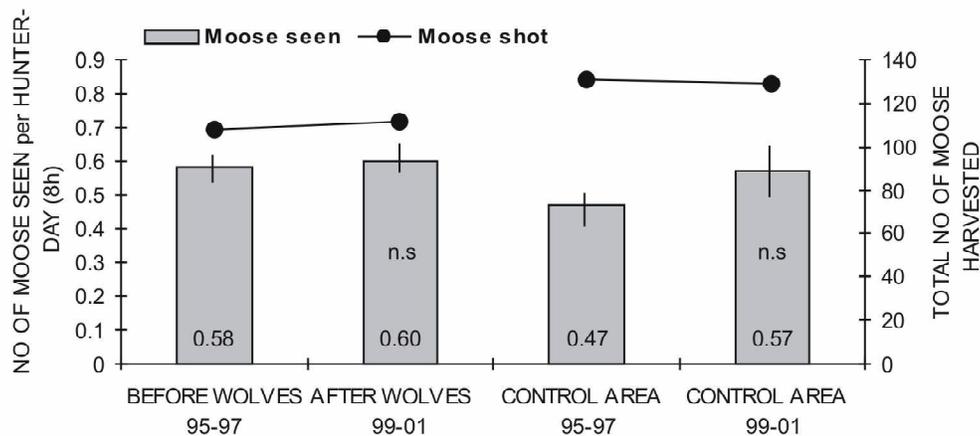


Fig. 3. Number of moose seen and harvested within a wolf territory and a control area, before and after wolf settled in the area in 1998, south-central Norway. Average winter density: 0.009 wolves and 1.5 moose per km². (n.s. = not significant.)

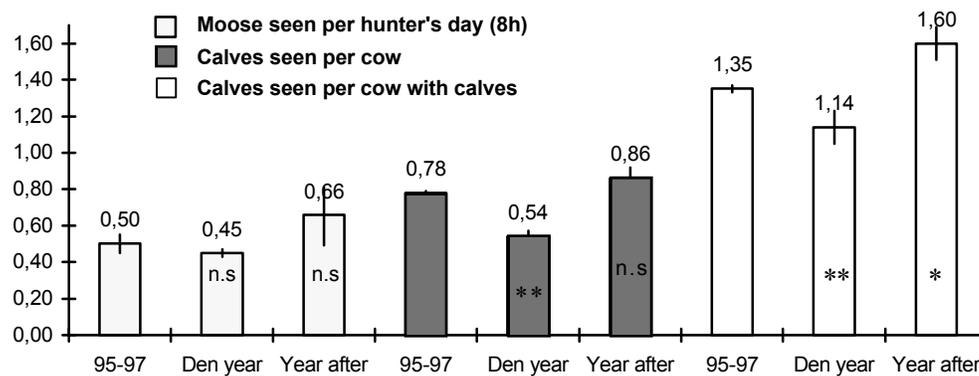


Fig. 4. Number of moose seen and calf recruitment rates in areas adjacent to the den in a wolf territory in south-central Norway. Data from 3 consecutive dens (1999-2001) are grouped. There were no wolves in the area prior to 1998. (n.s. = not significant.)

in the den areas significantly decreased in the years of wolf reproduction (from 0.78 ± 0.01 to 0.54 ± 0.03) ($t = 3.6$, 10 df, $P = 0.00$). The year after active denning, though, the c.c. ratios were higher than the pre-wolf levels (0.86 ± 0.08), but again the variance was high and the results were not statistically significant ($t = -1.0$, 10 df, $P = 0.17$).

If we look at only the cows with calves, fewer calves were seen per cow with calves in the den year than before wolf re-establishment (from 1.35 ± 0.02 before wolves down to 1.14 ± 0.03 in den year) ($t = 3.7$, 10 df, $P = 0.00$). As with the c.c. ratio, more calves were observed per cow with calves the year after denning compared to the period before wolves re-established (from 1.35 ± 0.02 to 1.60 ± 0.09) ($t = -2.1$, 10 df, $P = 0.03$).

DISCUSSION

Moose Calves in the Wolf Diet

Moose are the primary prey of wolves in the northern boreal forest (Fuller and Keith 1980, Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1991, Gasaway et al. 1992, Gade-Jørgensen and Stagegaard 2000). In our study, wolves clearly preferred the calf segment of the moose population during summer. A preference for calves was also shown by Olsson et al.

(1997) in south-central Sweden, where 51% of 65 moose killed by wolves were calves. Apparently low-density, colonizing wolves kill a higher proportion of calves than do established wolf populations (Fritts and Mech 1981, Boyd et al. 1994).

Smaller ungulates such as white tailed deer (Murie 1944, Carbyn 1983), red deer (Murie 1944, Carbyn 1983), caribou (Hollermann and Stephenson 1981, Dale et al. 1995), and roe deer (Olsson et al. 1997) seem to be the preferred prey where they occur together with moose. Our data suggest that roe deer were killed at about the same rate as moose during summer (36% of occurrence for roe deer, and 44% for moose). Since the density of roe deer probably was at least 3 times that of moose, this indicates a preference not for roe deer, but for moose. Scats collected on forest roads (May-November) in the study area and 2 other wolf territories in the same region, also indicate a preference for moose over roe deer during summer (Østreg 2000).

In Sweden, Olsson et al. (1997) concluded from their scat analysis, that wolves killed roe deer about twice as often as moose (52% of occurrence for roe deer, and 25% for moose). With a moose density in their study area at about 3 times that of roe deer, their conclusion was the opposite

of ours: that the wolves preferred roe deer over moose. In their study, however, scats were collected throughout the year. The relative vulnerability of roe deer to moose probably depends on seasonal factors such as snow depth. Furthermore, when the study in Sweden was started, moose had already been exposed to wolves for 7 - 8 years. This might have made the animals less naive as prey (Berger et al. 2001) compared to our study area where scats were collected shortly after wolves had settled in the area.

Expected Effects of Predation

Using data from the scat analysis, estimated moose density, yearly calf production, and wolf daily food requirement, we can estimate the effects of predation on this particular moose population: With 210 km² of moose habitat within the wolf territory, 315 moose (of which 105 were calves) were potential prey for the wolves each summer. There is no data in the literature to calculate the food needed to raise a litter of wolf pups. However, using data from Mech (1970) and data from dog breeders (Wam, unpublished data) we have set the average food intake by pups (average summer weight 9 kg) from mid May to the end of September at 1.4 kg per pup per day, and the average food intake for adults at 3.7 kg per animal per day.

A litter of 5 and 8 pups then needs 945 kg and 1,512 kg of meat, respectively, during the summer. In our study area, 61% of this should be derived from moose calves. Applying an average meat yield of 35 kg per moose calf (Olsson et al. 1997), and including the number of adult wolves (2 adults during the summer of 1999, 3 adults in 2000 and 2001) in our calculations, we estimate that 34, 40, and 50 moose calves were consumed over the summers 1999, 2000, and 2001, respectively. Within the den area of 2000 (5-6 pups), there were about 28

calves, given the moose density of 1.5 km², and in the den area of 1999 and 2001 (5 and 8 pups, respectively) there were 37, assuming that all of the area was moose habitat. Therefore, if wolves killed calves mostly within their den areas, very few if any would be left there by the end of the summer. For the territory as a whole, the estimated calf losses are 32, 38, and 48%, respectively, for 1999-2001.

Likewise, we can estimate the total number of moose killed since wolves first denned in this territory in 1999. Using the actual wolf pack size for each year, a daily meat intake of 3.7 kg per animal per day, and a similar proportion of calf and adult moose in the winter kill as in the summer kill, wolves should have killed an approximate total of 235 moose by the fall of 2001, or about 15% of the summer population per year.

Theoretical vs. Observed Loss from Predation

The observed overall losses of moose from predation were diminishingly small, and lower than expected from our theoretical calculations. Possible reasons include: (1) there was an increased immigration of moose into the territory; (2) more calves were born after the wolves established; or (3) the moose population was increasing at the time wolves re-established.

Theoretically the wolf territory could act as a sink for dispersing young moose from the surrounding forests. However, because the territory is enclosed by highways, lakes, and broad rivers, we believe the migration of animals into the area is negligible. Furthermore, there is little evidence showing a selective colonization by moose of areas where the density has been reduced from hunting, predation, or other causes (Hjeljord 2001).

An increase in calf production by cows losing nursing calves has been documented

in Scandinavian brown bears (Swenson et al. 2001), and this may also apply when calves are preyed upon by wolves. We found no decrease in the c.c. ratio in the territory at large after the wolves arrived, even though we did find a significant decrease within the den areas in the years of active denning. We speculate that this is partly due to higher fecundity in cows that lost a calf to wolf predation the previous year, as our data did show an increase in recruitment rates. However, our sample size is too small to draw any firm conclusion.

As calves in a den area are also preyed upon the year after active denning (albeit not that intense), increased fecundity in spring will be reduced by the time of census when using hunters' observations. The best way to assess the fecundity would therefore be to do a survey of the number of calves per cow as soon after birth as possible, and then compare it with hunter observations in the autumn.

For the control area, the hunter observations indicated an increase in the moose population from 1995 - 1997 to 1999 - 2001. The moose in the control area and the wolf territory have similar conditions, apart from wolf predation. Probably the wolves halted a similar increase in the moose population inside their territory and thereby masked some of the effects of predation.

The discrepancy between calculated and observed losses was enhanced by our assumption that the proportion of roe deer in the wolves' diet is similar during summer and winter. This assumption certainly is invalid for most winters, and this may be part of the reason why there has been a smaller impact of wolf predation than suggested by our estimates. This does not, however, affect what we observed.

south-eastern Norway caused little change to the highly productive moose population in the area. Yearly harvest and population size as indicated by hunter observations remained stable. We believe, however, that the moose population was increasing when the wolves settled, and this may have masked some of the effects of predation from wolves. If so, we will see greater predation effects in coming years as the increase is halted, and possibly reversed.

Our data also indicate that the moose might have compensated for the loss of calves during summer. It is, however, premature to conclude from our small sample size. More data is needed on this topic.

In our study area the wolves changed their den location from year to year. If this is something they ordinarily do, an area that is heavily preyed upon one year will get a chance to recover the following year, thereby dividing predation loss among land owners. However, over the long term and if hunting quotas are not adjusted, cohorts can be reduced below what is needed to replace harvested adult moose.

We have shown that hunter observation indices can be a valuable tool in future management of moose populations preyed upon by wolves in Scandinavia. They may be used to adjust hunting quotas for specific areas and years. To get an accurate account of the situation, though, it is important that the hunting units used as replicates are not too small. Rather than having many replicates, we believe it might be a better option to group small replicates into bigger units (within the appropriate geographical scale). Furthermore, data gathered by the hunters should be used to promote a good dialog between managers and the people who actually harvest the moose.

CONCLUSION

The establishment of a wolf pack in

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