THE IMPACT OF HUNTING ON MOOSE MOVEMENTS

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ABSTRACT: This study presents data concerning moose movements before, during and after hunting periods. We conducted the study in 1992 and 1993 in the Robertsfors area, in northern Sweden. A total of 50 animals (29 in 1992 and 21 in 1993) were located by radio tracking twice a day. All moose displayed a significantly higher rate of movement during day than night regardless of hunting activity ($P < 0.001$). Intense hunting activity affected the rate of movement of moose where cows with twins showed the most pronounced effect in this study. They increased ($P < 0.05$) their movement during day the intense hunting period. No correlation was established between movement and hunting mortality.

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There are two ways hunting may affect animals' rate of movement or activity patterns. First, the individuals may leave their original habitats. Two broad main strategies seem possible; (a) wildlife could move more and behave so as to increase their exposure to man or (b) they may exhibit a higher rate of movement over extensive areas. We found no evidence in the literature that supports the first strategy. Individuals could respond the opposite way, that is by decreasing their degree of exposure they would decrease the risk of detection by moving to areas free fromhunters. Mech (1977) and Edwards (1983) described examples where prey moved, or shifted habitat type, to predator-free environments thereby reducing mortality risk. Stephens and Peterson (1984) suggest that moose use this strategy during certain periods; particularly in winter, when the use of conifer forest may reflect an anti-predator strategy. Goddard (1970) investigated whether a heavily hunted area was repopulated by moose (*Alces alces*) from remote unhunted areas, but found no evidence to suggest that a directional movement into unhunted areas occurs. Nixon *et al.* (1991) found that white-tailed deer (*Odocoileus virginianus*) numbers increase in refuge areas and that, due to hunting mortality, individuals tend to settle in vacant areas. Gatti *et al.* (1989) reported a similar effect on habitat use by female pheasants (*Phasianus colchicus*), where the birds used larger home ranges during the hunting season and moved to their winter habitats earlier because of the hunting pressure.

Second, individuals can change their activity pattern in response to hunting. Skogland and Grovan (1988) followed two reindeer (*Rangifer tarandus*) herds exposed to hunting. The first herd (in good physical condition) responded by forming larger groups that became less mobile than before the hunt. The second herd (in poor physical condition) responded in the opposite way and became more mobile. To our knowledge no study has yet documented how moose response to hunting activity.

The objective of this study was to investigate how hunting affects the rate of movement of moose specific to age and sex category. Another objective was to see if the observation rate for moose, between the first hunting days in the Swedish National Moose Inventory is related to changes in the rate of movement.

STUDY AREA

We conducted the study in late August and early September 1992 and 1993 near Robertsfors (64° 12' N, 20° 45' E) in Västerbotten county (Fig. 1), in the northern part of Sweden. The landownership is a mix of small privately owned areas and larger areas owned by forest companies. The private hunting grounds are often aggregated to form larger areas during the hunt. In spite of that, the area covered by different hunting groups reflect the difference in landowner structure. For example, in 1991 13 persons (SD = 7) composed an average hunting group in the study area and covered an average of 2414 hectares (SD = 1877), whereas in 1992 hunting groups of 12 persons (SD = 8) covered on average 1765 hectares (SD = 1355). No data were available concerning the composition of hunting groups and area coverage in 1993. In 1992 the hunting season opened on September 7 and in 1993 on September 6, and ended December 31.

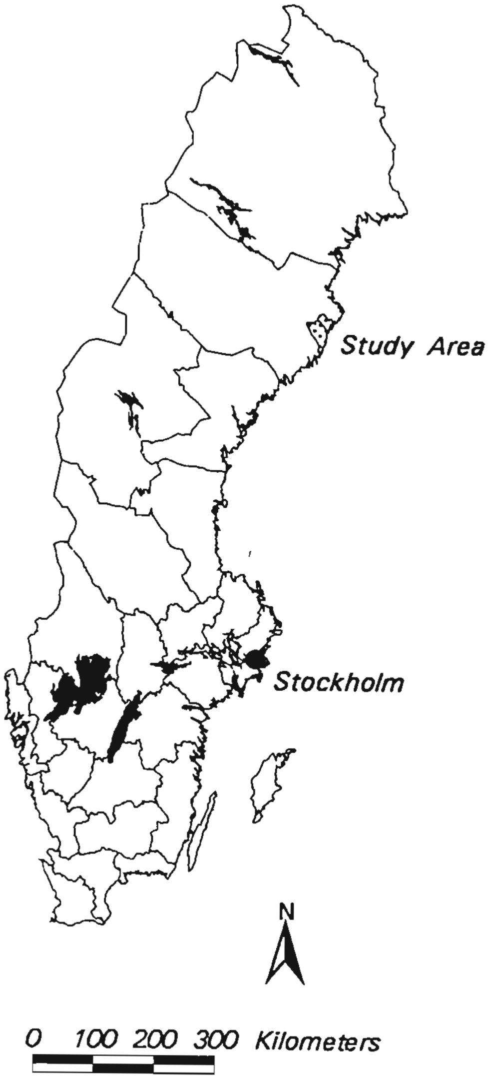

Fig. 1. The location of the study area Robertsfors (64° 12' N, 20° 45' E) in Västerbotten county, 600 km north of Stockholm.

Aerial surveys estimated the population density in the area at 0.7 moose per km^2 in the winter of 1990-1991. According to official hunting statistics for the Västerbotten county (Swedish Hunters' Association, 1995), the density of moose in the study area has shown an increase during the seventies and the early eighties peaking in 1983, but recently the population decreasing (Fig. 2) similar to that reported for Sweden (Cederlund and Markgren 1987).

The estimated annual harvest was about 30 % of the population in 1992. This estimate is based on the fact that hunters killed between 23% and 29 % of the marked individuals in this on-going moose study during the

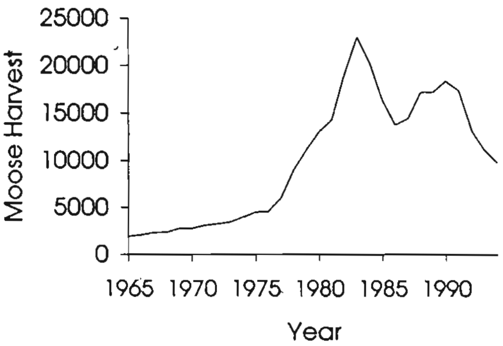

Fig. 2. Annual moose harvest in the county of Västerbotten, Sweden, from 1965 to 1994. Source: Swedish Hunters' Association, 1995.

1991 -1993 hunting seasons (Wallin and Ericsson, unpublished data).

METHODS

Prior to 1985 hunting season, hunters were asked to participate in a nation-wide moose-observation program, hereafter called the Swedish National Moose Inventory (SNMI). This initiative came from the Swedish Hunters' Association, an organization for Swedish hunters and is similar to observation programs currently ongoing in Finland and Norway. In these programs hunters collect information about the number of moose sighted during the hunting period. Hunters then categorize the observations as: bulls, cows with one or two calves, yearlings or unidentified individuals. They also report how many hunters have participated and record their hunting efforts in days or hours. The initial aim of this inventory is to monitor changes in both numbers and population structure (Thelander *et al.* 1986).

In the study area, moose were fitted with radio collars since 1990 as a part of a larger moose project. In 1992, 45 moose were instrumented with radio-collars and by August 1993, 104 moose were collared.

All the individuals were categorized into four groups (bulls, cows with one calf, cows with twins, and single females), which coincides largely with how the Swedish hunters report to the nation-wide SNMI. The standard classifications made it possible to compare the rate of movement of moose in the latter inventory to that reported by the hunters.

Among the 45 individuals in 1992 we selected a stratified sample of 29 animals for the study; four bulls, eleven single females, ten cows with one calf and four cows with twins. The ages ranged from one to ten years old (mean age = 5.6, SD = 2.7). In 1993 we selected 24 individuals from the 104 marked individuals; ten bulls, three single females, three cows with one calf and eight cows with twins. Later, three individuals had to be excluded from the analysis, because no hunters were active in their areas. The ages ranged from one to ten years old (mean age = 5.0, SD = 3.1). The two samples had an even age distribution.

We followed the individuals intensively by radio tracking Monday through Friday during the pre-hunt week, and Monday to Friday during the first week at the hunt. Each individual was located twice daily with at least six hours between each record, but this was not always met for practical reasons. The locations were plotted by triangulation of three bearings. If the bearings calculated did not produce an exact position, we minimized the area of the triangle to the given bearings in order to better accuracy a location within one tenth of a square kilometer. In 1992 89 % of the locations met this criteria and 39% were exact positions. In 1993 97 % met the criteria and 39 % of the locations were exact. We considered the center of the triangle to represent the position of the individual.

Because estimates of movement are by telemetric plots of intermittent records of animals, the actual distance moved by moose may have exceeded the distances between consecutive radio locations. Thus, estimates of moose movement are likely conservative estimates of the actual distance covered by moose. The linear distance between each consecutive location was calculated by the Pythagorean theorem, $d = ((x_1 - x_2)^2 + (y_1 - y_2)^2)^{0.5}$, where d = linear distance, y_n = latitude, x_n = longitude. Since the time between each location varies, each distance was divided by time in order to facilitate a comparison of rate of movement of individuals and categories in meters per hour (m/hr).

The non-parametric tests: Kruskal-Wallis (Siegel and Castellan, 1988), Wilcoxon matched pairs signed ranks (Siegel and Castellan, 1988) and Wilcoxon rank sums (SAS, 1989) were used for the analyses because movements are not normally distributed. The use of Wilcoxon matched pairs signed ranks enabled us to use each individual as it own control.

RESULTS

Variation in rate of movement between 1992 and 1993

There were no significant differences found ($P > 0.27$) in the rate of movement between the two years (Wilcoxon rank sums test) for individuals and all categories. Also, when we split the rate of movement into rate of movement during night and day, no significant differences ($P > 0.14$) were found between years where "night" is defined as the time between the last location (afternoon or evening) of the day and the first location (morning or pre-noon) the following day.

All moose and moose by categories had a significantly higher rate of movement during the day (both weeks pooled, Kruskal-Wallis test, $P < 0.001$). Considering each category, we found that cows with one calf showed a higher daily rate of movement in 1992 ($n = 10$, mean$_{92}$ = 92.6, SE = 24.1, Kruskal-Wallis test, $P = 0.039$) compared to 1993 ($n = 3$, mean$_{93}$ = 55.2, SE = 25.0) and that cows with twins had a higher rate of movement during night time in 1992 ($n = 4$, mean$_{92}$ = 51.2, SE = 22.9, Kruskal-Wallis test, $P = 0.049$) compared to 1993 ($n = 7$, mean$_{93}$ = 34.8, SE = 10.8).

Because there were no general differences between the years, we pooled the data from the two years. Small sample sizes ($n = 3$ and $n = 4$) precluded separate analyses for cows with one calf (1993) and cows with twins (1992).

Differences in rate of movement between the pre-hunting and hunting week

When we compared the means for all moose (without splitting into day or night movement) from the week without hunting activity and the week with hunting activity, we found no significant effects on movement ($P > 0.94$, Wilcoxon signed matched paired rank test, $n = 50$). The same insignificant results were found on the category level (Table 1), Wilcoxon signed matched paired rank test, n = 13, 11, 14, 12 and T = 37, 27, 46, 39 respectively, $P > 0.05$. Cows with calves and adults without calves were also unaffected (Wilcoxon signed matched paired rank

Table 1. Average rate of movement (m/hr) and standard error (SE) for categories of moose during three periods.

Category	Pre-hunt	Intense hunt	Less intense hunt
Cow + 1 calf (13)	64.4 (7.1)	69.2 (11.0)†	56.8 (6.1)†
Cow + 2 calves (11)	62.5 (4.5)	102.7 (29.7)**	53.3 (10.5)**
Females (14)	87.8 (10.4)	85.7 (11.7)	79.1 (14.4)
Bulls (12)	83.0 (7.5)	88.4 (16.5)‡	109.5 (21.8)‡
All individuals (50)	72.5 (3.6)	86.0 (8.8)†‡	73.8 (7.4)†‡

†= One cow excluded (shot), ‡ = two bulls excluded (shot), **=significant at $P <= 0.05$.

test, $n_{cows} = 24$, $T = 151$, and $n_{adults} = 26$, $P > 0.88$). All females (with and without calves) and bulls were pooled together into separate groups and the same effect: hunting did not affect the rate of movement (Wilcoxon signed matched paired rank test, $n_{females} = 38$, $P > 0.83$, $n_{bulls} = 12$, $T = 39$) of either group.

We also divided the hunting week into two periods, (Monday to Tuesday, and Wednesday to Friday) and compared them with the week without hunting. The division reflects the higher hunting effort (hrs/km^2) the two first hunting days (Fig. 3). There were no significant differences in the rate of movement between the week without hunting and the two periods of the hunting week, when comparing each category and when comparing for all moose (Table 1, Wilcoxon signed matched paired rank test, $n = 47$, $P > 0.28$). However, when we compared the two periods of the hunting week cows with twins moved greater distance than all other categories during the period of intense hunt (Table 1, Wilcoxon signed matched paired rank test, $n = 11$, $T = 11$, $P < = 0.05$).

Also, there was no impact on the rate of daily or nightly movement during the pre-hunt and the first week of hunting for all moose and all categories (Wilcoxon signed matched paired rank test, $P > 0.54$, $n = 50$).

When we divided the hunting week by hunting effort (Fig. 3) the average daily rate of movement (Table 2) of cows with twins (131 m/hr to 57 m/hr, Wilcoxon signed matched paired rank test, $n = 11$, $T = 7$, $P < =$

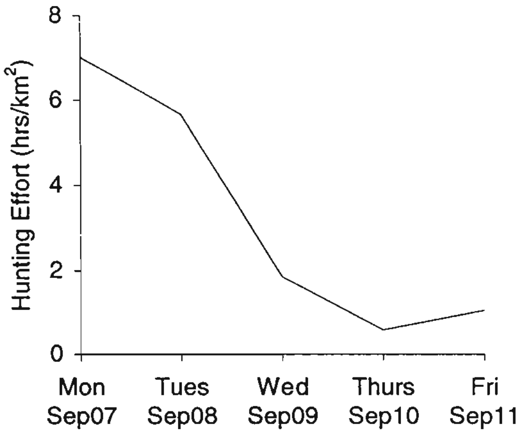

Fig. 3. Hunting effort (hrs/km^2) spent by the hunters in the study area during the first week in September 1992. No data were available for 1993.

Table 2. Average rate of movement (m/hr) and standard error (SE) for different categories of moose during night and day for the week before the hunt (pre-hunt), and for two periods during the first hunting week. The differences between day and night are significant (Kruskal-Wallis test, $p < 0.001$).

	DAY			NIGHT		
	Pre-hunt	Intense hunt	Less intense	Pre-hunt	Intense hunt	Less intense
Cow + 1 calf (13)	89.2 (18.2)	96.0 (14.1)†	86.2 (11.6)†	42.4 (5.8)	30.5 (7.3)†	36.9 (4.7)†
Cow + 2 calves (11)	79.7 (6.5)	130.5(33.4) **	57.4 (8.4) **	47.4 (5.1)	37.8 (9.7)	38.5 (7.3)
Females (14)	111.1(24.9)	101.6(12.9)	103.1(44.7)	53.4(9.6)	39.4(9.3) **	65.4(10.8) **
Bulls (12)	107.1(10.9)	115.1(26.4)‡	102.3(17.3)‡	51.2(5.6)	57.0(16.8) ** ‡	91.8(23.2) ** ‡
All individuals (50)	95.6(7.9)	110.9(11.7) ** †‡	85.7(11.4) ** †‡	48.3(3.2) ** †‡	41.0(5.7) ** †‡	56.1(6.4) **

† = One cow excluded (shot), ‡ = two bulls excluded (shot), ** = significant at P <= 0.05.

0.05) and for all moose (111 m/hr to 86 m/hr, Wilcoxon signed matched paired rank test, n = 47, P = 0.038) decreased significantly between the two periods of the hunting week (Fig. 4). The observed increase, 96 m/hr to 111 m/hr between the week before the hunt and the days with intense hunt for all moose has a P-value of 0.052 (Wilcoxon signed matched paired rank test, n = 47).

For the nocturnal rates of movement (Table 2) we found four significant differences (Fig. 5). Moose move less when the hunt is intense when compared to the week without hunting (41 m/hr respectively 48 m/hr, Wilcoxon signed matched paired rank test, P = 0.032) and move more when the hunting is less intense compared when hunting is intense (56 m/hr respectively 41 m/hr, Wilcoxon signed matched paired rank test, P = 0.012). Bulls and females without calves show a similar significant increase between the two periods the hunting week. Bulls increase their rate of movement from 57 m/hr to 92 m/hr (Wilcoxon signed matched paired rank test, n = 8, T = 3, P < 0.05) and females (without calves) increase theirs from 39 m/hr to 65 m/hr (Wilcoxon signed matched paired rank test, n = 9, T = 6, P < = 0.05)

Differences in rate of movement between categories

Females without calves have the highest average rate of movement (88 m/hr) during the pre-hunt week (Table 1), followed by bulls (83 m/hr), cows with one calf (64 m/hr) and last cows with twins (63 m/hr). At least one category differs significantly from the other three (Kruskal-Wallis, chi-square = 8.44, df = 3, P = 0.038). If one considers the whole hunting week there is no significant difference between the categories' rate of movement. During the period with more intense hunting there is no significant difference between the categories average rate of movement (Kruskal-Wallis, chi-square = 1.53, df = 3, P = 0.675), but the period with less intense hunt shows the same significant relationship as the pre-hunt week (Kruskal-

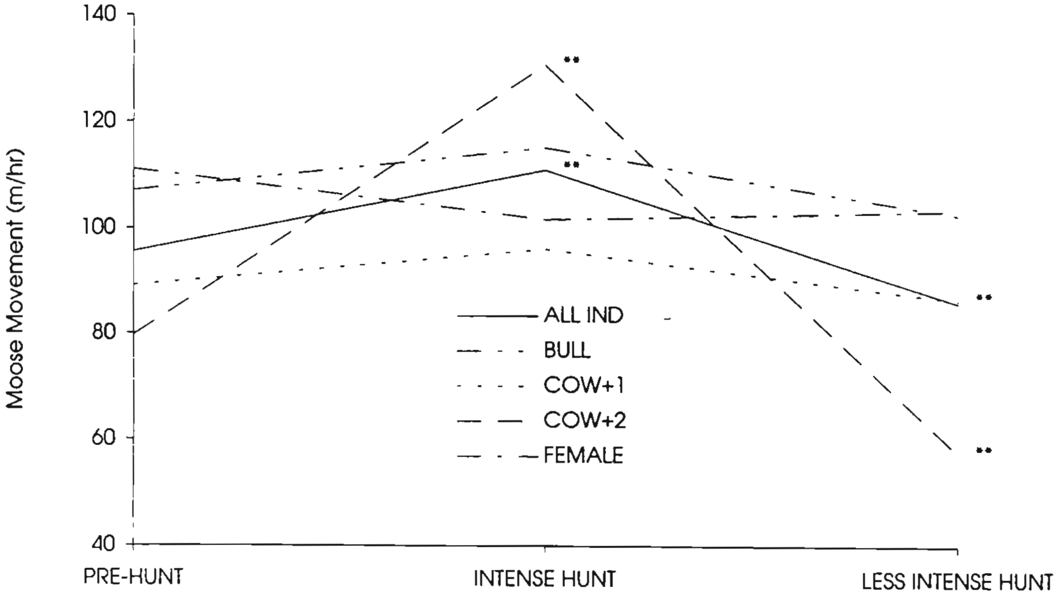

Fig. 4. Average rate of daily movement (m/hr) for categories of moose.

** Indicates significant changes between periods (Wilcoxon signed matched paired rank test, P <= 0.05).

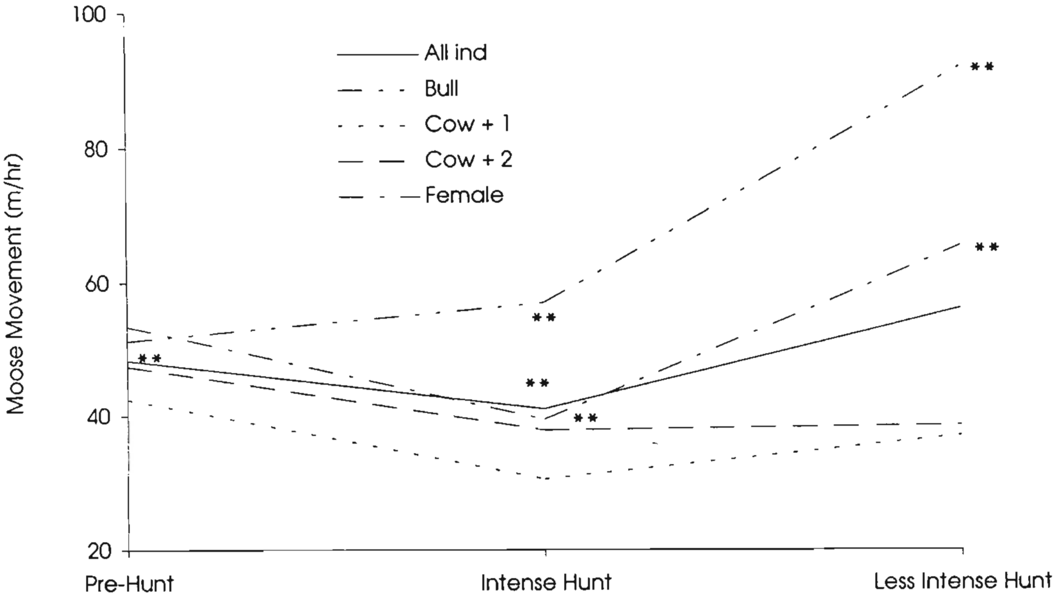

Fig. 5. Average rate of movement during night (m/hr) for categories of moose.

** Indicate significant changes between periods (Wilcoxon signed matched paired rank test, P <=0.05).

Wallis, chi-square = 8.67, df = 3, P = 0.034). So what happens when the hunting is intense in each category's average movement rate that causes this? The main effects seem to be that cows with twins increase their rate of movement and bulls decrease theirs compared to the other categories during the other two periods. There are no significant differences between the categories' rate of movement when the hunting is intense.

Directional movement during the hunt

During the hunting week 1992, 11 (2 bulls) of the 29 individuals showed a directional movement (mean = 2775 m, range 971-6760 m) away from where they were located before the hunt, which we define as the range they had been frequenting since the beginning of July. Six of them showed a movement pattern during the hunting week that suggested they were moving back towards their previous area of residency.

In 1993, 7 (3 bulls) of the 21 individuals displayed a directional movement (mean = 1872 m, range 1221-3847 m) away from the area they were occupying before the hunt. Two of these animals moved towards their previous area of occupancy prior to the hunting period.

Movement and hunting mortality

No significant correlation was established between the rate of movement and mortality during the hunting week (Wilcoxon rank sums, P = 0.15). Bulls that were shot had an average rate of movement during the hunting week of 116 m/hr (n = 6, SE = 28) compared with the ones that survived which on average had a movement rate of 82 m/hr (n = 6, SE = 16). No relationship was detected between age and rate of movement for all categories, however.

DISCUSSION

One of the main problems when discussing impact of hunting on movements of moose is to determine what is the "normal" rate of movement. How would an undisturbed moose have moved? Possibly different needs trigger movement for in different categories of moose, but it is reasonable to think that foraging plays an important role. Moose not affected by hunting remain in an area for a while, and then do a longer directional move, so sooner or later it will leave the area (Riesenhoover 1986, Wallin 1994, unpublished material.).

The observed pattern that bulls and females had higher movement rates than cows with calves, when not disturbed or when the hunt was less intense, may be due in part to differences in forage distribution (quality or quantity). Bulls during this period forage possibly to build up reserves to meet energy demands for the rut. Riesenhoover (1986) found that when moose foraged longer, the linear distance travelled also increased. He also reported that "seasonal changes in levels of activity appears to reflect behavioural and physiological adaptations of moose to temporal changes in forage quality and patterns of forage distribution".

For a cow with calves, the best strategy is to remain in a good foraging area. Once in these foraging sites, the cow might maximise her energy intake and at the same time minimise the energy expenditure of the calves. The cow and calves would remain in the same area for as long as the forage is better than found elsewhere (Charnov 1976). An alternative explanation for the low rate of movement of maternal cows might be attributed to predator avoidance. For example, Edwards (1983) reported that maternal cows moved to relatively predator free areas. However, we think this is unlikely in our area because the only potential predator is man and therefore the only period when the individuals must avoid predation is during the hunt.

What then is the best strategy to use for a moose encountered by hunters? Clearly, it has two options: stay in the area, or move and expose itself. As long as it is not discovered the best thing is to remain in seclusion. Is the risk of discovery the only thing that will make a moose move? The response to move could also be the result of disturbance. It is possible that the different categories may respond differently when disturbed.

Before the hunt, cows with calves were the least mobile category compared with females and bulls (Tables 1 and 2). During the intense hunting period all categories, when combined, increased their rates of daily movement. Before the hunt, and during the less intense hunt, there was a significant difference between the category's average rate of movement with bull and single females being the most mobile. During the period with intense hunting all categories displayed the same movement pattern. As a conclusion one could say that hunting influences *the pattern* that was observed before the hunt in all categories and that hunting intensity affects moose mobility.

That hunting at least has some effect on movement becomes clearer when looking at day and night movement. All categories of moose, when combined, displayed higher movement rates during day with intensive hunting than during the night. Hunting especially influences cows with twins which have a significantly higher rate of movement during day time when the hunting is intense compared with the less intense period. In fact, they also have the highest movement during the day during this period in comparison to all other categories (Table 2).

Why do cows with twins have a higher rate of movement than other categories of moose? First, if it is more likely that hunters discover cows with twins, then they are also more likely to be disturbed and thus move around more. Some hunters claim that when they hunt with dogs, they more often encounter cows with calves. It could be due to the fact that a larger group either leaves more scent and or uses a relatively larger area, which would then increase their risk of being discovered. Second, cows have made a large reproductive investment and to best protect their calves, they may leave the area occupied with hunters (predators) to a relatively predator-free area in their home ranges. Third, if larger groups of moose can effectively sense dogs or hunters approaching them better than individuals (Hamilton 1971), then they would likely show a higher rate of movement. Or, perhaps maternal cows are more alert to the presence of hunters and their hunting activity.

We suggest that the lower movement rates observed for females and cows with calves during night the intense hunting period, is a response to the higher rates shown during day time. It is plausible to think that they have to forage more during night time, partly to compensate for lost foraging time during the day, and partly to compensate for increased energy expenditure due to higher rate of movement. The higher rate of movement observed for bulls during the hunting week is difficult to isolate from the effects of the approaching demands of the rut. Bulls have a higher rate of movement during the mating season and there is some evidence that most movement occurs during day time in the early rut (Riesenhoover 1986). The higher movement rates could also be related to larger home ranges of bulls in the fall. Gustafsson (1992) states that, in the fall, bulls use on average home ranges that are 3.5 times larger than cows. If older males move more during the hunt, it may lead to higher hunting mortality though our present data does not support this. The onset of the mating season could also explain the higher rate of movement for single females during the less intense hunting period. Besides hunting effecting rate of movement, hunting seems not to make individuals leave their July and August home range permanently. Some individuals displayed a directional movement during the hunt, but to isolate that from normal movement is difficult. Moreover, the hunting pressure was likely below some threshold of disturbance that individuals did not permanently move to a new home ranges; but rather moved to an area of little hunting activity within their familiar home range. Gustafsson's findings (1992) that moose show a high degree of fidelity supports this observation.

In conclusion; it seems that hunting influences the rate of moose movement. Although, the effect does not seem to be strong, intense hunting seemingly influences moose cows with twins. The hunting pressure monitored in this study might be below some disturbance threshold to produce any stronger effects. However, our results do not support the view that moose tend to decrease their rate of movement during the first days of hunting and thereby influence the observation rate in the SNMI.

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