



# Moose group-size: a sex-specific strategy when faced with wolf predation risk

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Marie-caroline PRIMA  
marie-caroline.prima@agroparistech.fr



**Grimso wildlife research station, Riddarhyttan**  
**Swedish University of Agricultural Sciences, Dep of Ecology**

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Supervisors : Johan Mansson and Kerry Nicholson

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# 1 Introduction

Presence of predators tend to shape and strongly impact prey behaviour such as feeding choice, movement patterns, sociality, vigilance and group characteristics (Lima and Dill, 1990). Anti-predatory responses by prey to the risk of predation may include changes in vigilance (Holmes, 1984; Lima, 1995; Laundre et al., 2001), habitat selection (Creel et al., 2005; Stephens and Peterson, 1984), movement patterns (Gude et al., 2006), distribution (Gude et al., 2006; White et al., 2012) and sexual segregation (Miquelle et al., 1992). Moreover prey may change their grouping behaviour as it has been shown in mammals (Heard, 1992; Lipetz and Bekoff, 1981; Lagory, 1986; Shi et al., 2010), birds (Powell, 1974; Bertram, 1980) and some fishes (Magurran et al., 1985).

Anti-predatory strategies are sometimes costly. An individual may have to choose a predator avoidance behaviour thus giving up the opportunity to obtain other resources. An individual cannot simultaneously feed and continually scan its environment to detect the presence of predator (Lima, 1996). Since an animal cannot be solely devoted to predator avoidance, there must be a trade-off between safety behaviours and behaviours that allow the animal to obtain resources needed to survive and reproduce (Lima, 1998). Group living is one behavioural response option, yet it too has a cost. Larger groups have a higher probability to be detected by a predator, thus they are subject to higher attack rate (Vine, 1971). Additionally, by being in a larger group they suffer a higher level of resources competition (Janson and Goldsmith, 1995; Molvar and Bowyer, 1994).

Conversely, there are anti-predatory benefits of group living which have been hypothesized and supported by in the scientific literature for a wide variety of species. Unglaub et al. (2013) found that large groups of crab spiders (*Diaea ergandros*) had a lower mortality risk compared to groups of small and middle size when faced to the risk of predation by clubionid spiders (*Clubiona robusta*). Similarly, three-spined stickleback (*Gasterosteus aculeatus L.*) showed a decrease in the success of attack on larger groups of daphnia (*Daphnia magna*), due to a decrease in the accuracy of each attack (Ioannou et al., 2008). These results support the hypothesis that group-living individuals benefit from confusing the predator when engaging an attack (*confusion hypothesis*, Milinski, 1977). The theory of the confusion effect has also been examined in fish (Landeau and Terborgh, 1986) where studies showed a reduction of successful predator attacks with an increase in prey group-size.

The decrease in the attack success of stickleback on large groups of daphnia can also be explained through the *many-eyes hypothesis* which supports another positive association between group living and anti-predation strategy. Individuals in a foraging group can spend less time being vigilant and the proportion of vigilant individual can decreases with the increase of the group-size. As group-size increases, there are progressively more eyes scanning the environment for predators

(Lima and Dill, 1990). Thus an individual forager can devote less time to vigilance and more time to feeding (Lima, 1995). Even though the individual vigilance in group is lower, the detection of a predator is more efficient and occurs earlier (Roberts, 1996).

Hamilton (1971) proposed an other theory explaining the beneficial effect of large group formation as an effective anti-predator response: the *selfish herd hypothesis*. Observations showed that the predators often capture isolated or marginal individuals. This is reasonable considering the threat of predation is likely to come from the direction of approach which is often outside the group formation. Thus, as the selfish herd theory proposes, individuals in the center of the group are more protected from predator attacks than outermost individuals leading to large and compact herds (Hamilton, 1971). Besides, individuals at the central positions can devote more time to feeding than being vigilant as observed in Przewalski's gazelle (*Procapra przewalskii*) (Shi et al., 2010) and pronghorns (*Antilocapra americana*) (Lipetz and Bekoff, 1981).

Heard (1992) showed that musk-ox (*Ovibos moschatus*) group-size increased with an augmentation of wolf (*Canis lupus*) density. Musk-ox group-size were larger during winter when wolves preyed more on ungulates than during summer (Heard, 1992). Since prey with the same physical conditions have the same probability to be selected by a predator, it seems intuitive that the larger the group, the lower the probability for each prey within the group to get caught. Thus, group-living individuals are protected through dilution (Foster and Trehern, 1981; Wrona and Dixon, 1991).

Grouping behaviour is commonly explained as an anti-predator response because of its advantages returned; however, this is nonetheless species dependent. For instance, an unexpected result observed in a population of elk (*Cervus elaphus*) in Montana noted elk grouping in larger herds when wolves were absent, which is thought to be explained for foraging reasons (Creel and Winnie, 2005). Another survey on the same species conclude that elk adopt two different strategies to minimize predation risk : either they choose to live in small herds that were rarely encountered by wolves or they choose to live in large herds that reduced their predation risk through dilution (combining benefits from the selfish herd and many eyes hypothesis) (Hebblewhite and Pletscher, 2002). Similarly, the Alaskan moose (*Alces alces gigas*) displayed plasticity by electing either to form a social grouping pattern or to stay solitary to avoid predation (Molvar and Bowyer, 1994). They increased their group-size with distance from cover, especially small groups (one or two moose) tended to stay close to cover. This pattern of grouping behaviour could be explained as anti-predation response since larger groups were observed in riskier places and small groups or solitary moose stayed hidden (Molvar and Bowyer, 1994). However, Alaskan moose increased its group-size as an anti-predator response but at the cost of reduced foraging efficiency because of increased social aggression (Molvar and Bowyer, 1994).

Relaxation of predation pressure over time can have behavioural consequences (Berger, 1999). However, the time before you see a behavioural effect in relation to changed predation risk varies between studies. Berger (1999) found that desensitizations in predation pressure can occur in less than ten generations as it is the case with pronghorns and musk-ox which decreased group-size in no more than 50 years after relaxation of predation. Berger et al. (2001) also found that preys that had been unfamiliar with predators for as few as 50 to 130 years were highly vulnerable to initial encounters but behavioural adjustments to reduce predation occurred within a single generation; compared to female moose (*Alces alces*) who reared their offspring successfully, female who had their calves killed by recently reintroduced wolves increased their vigilance and changed their calving site the next year. However, behavioural readjustment after predator re-establishment may take longer or be nonexistent as it is the case for male elk in Yellowstone National Park who did not show any increase in vigilance 5 years after wolves re-establishment whereas female with or without calves gradually increased their vigilance levels in wolf areas (Laundre et al., 2001).

Predation risk is not the only environmental variable that may influence group-size and formation for animals. Weather conditions such as snow cover have explained the grouping behaviour of musk-ox which were observed in larger groups during winter (Heard, 1992). Snow cover decreases food availability and creates limited and irregular food patches, thus individuals tend to stay together in areas providing high energy intake (Heard, 1992; Gude et al., 2006). Furthermore, snow reduces ungulates movements (Coady, 1974) and increases their vulnerability to predation (Huggard, 1993; Gervasi et al., 2013). It has been shown that individuals reduce their predation risk by either avoiding deep snow areas (Peek et al., 1974; White et al., 2012) or by increasing even more the group-size in snowy areas to augment their chance of survival (Heard, 1992).

Hebblewhite and Pletscher (2002) showed that elk group-size was positively correlated to elk density. Group-size response to elk density was sex-specific: group-size increased with elk density for both sexes but females tended to be in larger groups than males (Vander Wal et al., 2013). In addition, Alaskan moose showed variation in group-size in accordance with group composition (Peek et al., 1974; Molvar and Bowyer, 1994; Miquelle et al., 1992). For example, females with calves stayed apart from other moose (Miquelle et al., 1992; Peek et al., 1974).

Because ungulates displayed a wide variety of responses in anti-predatory behaviour world wide, I have been interested in studying grouping behaviour response of one ungulate to the re-establishment of predation pressure. In Scandinavia, the wolf was functionally extinct by 1966 but recolonization occurred and by 1983, wolves were documented as successfully breeding (Wabakken et al., 2001). In south-central Scandinavia moose have not experienced wolf predation for 120-150 years (Sand et al., 2006a) and they are the main prey of wolves (Olsson et al., 1997).

My study objectives were to determine moose spatial grouping pattern in Scandinavia in

response to the recolonization of wolves and how predation risk is important in moose grouping formation. I used winter aerial moose survey data to determine if Scandinavian moose inside and outside wolf territories employ different grouping strategies. In addition to wolf risk, I evaluated other factors that may influence grouping behaviour such as prey density, latitude, snow depth and group composition. I predicted that group-size will change in response to wolf exposure. I also expected different grouping strategies in Scandinavian moose depending on age and sex composition of the group.

## 2 Materials and Methods

### 2.1 Study area

The study area encompasses 50000 km<sup>2</sup> of south-central Sweden (Figure 1, 58.58° - 62.16°N; 13.45°-16.64°E). It is a boreal zone with a domination of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) but also deciduous trees, such as birch (*Betula spp.*), aspen (*Populus tremula*), alder (*Alnus incana*) and willow (*Salix spp.*). The forest is intensively managed for timber and pulp. Mature stands are harvested by clear-cutting and reforested by planting or natural regeneration, resulting in even-aged forest stand mosaic ([www.skogsstyrelsen.se](http://www.skogsstyrelsen.se)).

Most precipitation falls during summer in June, July and August when the mean of rainfalls varies between 50 and 70 mm/month. Average temperature ranges between +22°C and -14°C with the coldest month in January and the warmest month in July ([www.smhi.se](http://www.smhi.se)). Snow covers south-central Sweden for 3 to 6 months each year and snow depth in the study area commonly ranged 0-75 cm in mid-winter.

Moose density throughout all of Sweden averaged less than 1.0 moose/km<sup>2</sup> but within study area the moose density included 1.9 moose/km<sup>2</sup> (Lavsund et al., 2003). Moose population is intensively harvested in Sweden, resulting in a female biased population with a sex ratio female:male approaching 1:0.7 and thereby a high productivity (Lavsund et al., 2003).

Three other ungulates occur in low density within the study area; roe deer (*Capreolus capreolus*) are distributed over the whole study area, red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) only occur in some parts of the area (Liberg et al., 2010).

The bear (*Ursus arctos*), is the only other important carnivore that predated on moose in Sweden but they are absent from the study area (Huber, 2013).

I have moose observations from winters 2006, 2009 and 2011. Between 2006 and 2009, the wolf population increased considerably: 15 wolf packs and 14-15 wolf pairs were estimated in 2006, in 2009 the population was estimated at 28 wolf packs and between 11 and 15 wolf pairs

([www.rovdata.no](http://www.rovdata.no)). In 2011, wolf population was estimated at 31 wolf packs and between 27 and 30 wolf pairs ([www.rovdata.no](http://www.rovdata.no)). Wolf range covers 100 000 km<sup>2</sup> in both countries Sweden and Norway but most of the wolf population occurs in Sweden (38 packs and 26 scent marking pairs in 2012) (Liberg et al., 2012; Chapron, 2013).

## **2.2 Moose aerial counts**

I obtained 1335 moose observations from Svensk Naturförvaltning, 782 were collected by aerial count from square samples (Ronnegard et al., 2008) and 553 by distance sampling (Thomas et al., 2010). The aim of those inventory campaigns is to estimate moose density in different areas of Sweden in order to set hunting quotas and reach management goals ([www.naturforvaltning.se](http://www.naturforvaltning.se)). The moose surveys were conducted during periods of snow for increasing detectability and were performed in mid-Dec to mid-Feb. In the analysis I did a pairwise analysis with data obtained from the same method to compare moose group-size inside and outside wolf territories.

For each observation, GPS-position, number of male, female and young moose were recorded. Bulls were identified by presence of antlers or antlers scars and lack of the white vulvar patch, cows were identified by lack of antlers or scars and presence of the white vulvar patch and calf was recognized on a basis of size and the short snout characteristic of young-of-the-year.

## **2.3 Monitoring of wolves**

I used location data on wolves monitored within the ongoing monitoring of Scandinavian wolf population ([www.viltskadecenter.se](http://www.viltskadecenter.se)) during winters 2006, 2009 and 2011. Seventeen wolf territories were included in the survey (Appendix A). Among those 17 territories, 10 were monitored yearly between October 1 - February 28 by snow tracking (Liberg et al., 2012). Sweden is divided in 21 counties (administrative regions), each county is responsible for performing annual snow tracking monitoring of wolves. Between 5 and 15 rangers per county track the wolves. When they find tracks, especially when it is 2 or more wolves, they backtrack for at least 3 km or even longer if possible. From this backtracking, they estimate pack size, record territorial scent markings, collect oestrus bleedings and scats for DNA-analysis. Wolf territories are classified in different categories: family group (3 or more wolves), territorial pairs, other stationary wolves (individual wolves that have recently settled, or stayed after family groups division) and vagrants (for further details regarding methods and protocols see Liberg et al., 2012).

In addition to snow tracking, over the years several wolves have been radio-collared. I used radio-tracking data for 7 wolf territories to estimate territory range (Appendix A). Wolves capture

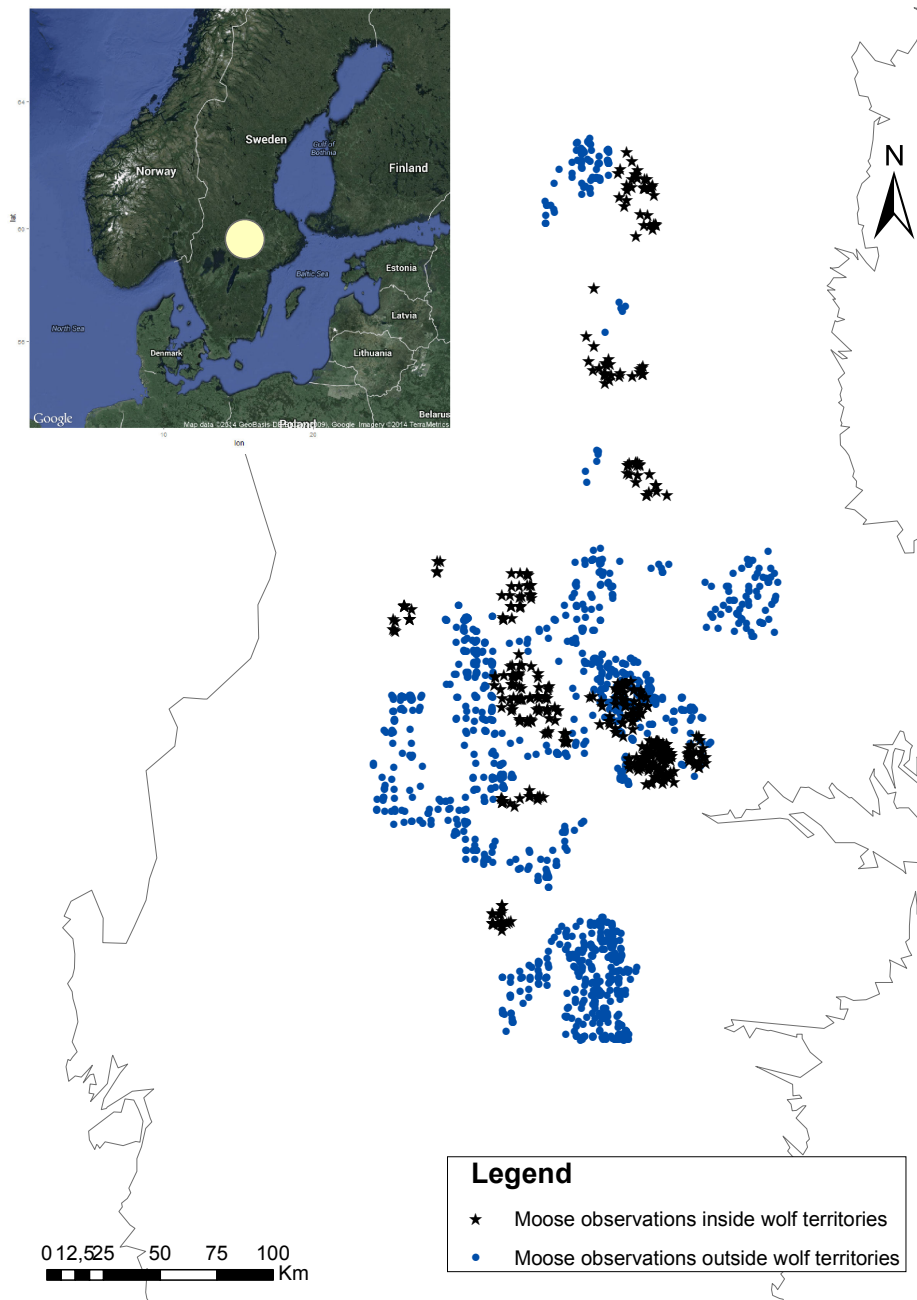


Figure 1: Location of the study area : south-central Sweden. Red and green dots represent moose observations inside wolf territories and outside wolf territories respectively, in Sweden from survey data collected in 2006, 2009, 2011.



and equipment is also managed by the Scandinavian Wolf Research Project (for further details regarding capture see Liberg et al., 2012 and Sand et al., 2006b). Positioning frequency depends of the season but at least one location is taken per day. Radio-collared wolves are also snow tracked using the same methods and protocols that the rangers for backtracking uncollared wolves to estimate pack size and pack composition.

## 2.4 Classification

With GPS position of collared and snow tracking data of non-collared wolves I estimated wolf territory range by using a 100 % minimum convex polygon (MCP) estimator (Mohr, 1947). Since non-collared and VHF-collared wolves were monitored during a limited portion of the year I buffered each territory (Appendix A) as a conservative approach to ensure that moose observations were actually outside any wolf territory. In order to limit data removal, I buffered each territory on a case by case basis. The buffered zone was estimated by two different methods: for MCPs estimated from snow-tracked wolf territories I buffered the territory so that the size of the buffered territory equaled the maximum wolf home-range observed in Scandinavia (i.e. 1700km<sup>2</sup> based on GPS-data, see Mattisson et al., 2013). Radio-tracked wolf territories were buffered according to the proportion of annual home-range size (Appendix A). This proportion was estimated with the number of months included in radio-tracking data (varied between 4 and 7 months, Appendix A; see Mattisson et al., 2013 for details).

Since home-range size varies considerably from one wolf territory to another (Mattisson et al., 2013; Liberg et al., 2012) I considered only moose observations that were clearly inside the MCPs based on tracking and GPS data as inside (i.e. wolf presence) and positions outside the MCPs and buffer zone as outside (i.e. wolf absence). Moose observations within the buffer zones were removed from the data set.

Furthermore, I only kept moose observations from inside resident wolf territories, thus I did not consider moose observations within stationary wolves territories or vagrants wolves; therefore, I only analyzed moose observations within family group territories or established pair territories.

I considered each moose observation as a group and I combined observations that were within 100m (Sweanor and Sandegren, 1986; Profitt et al., 2008). I did not consider calves in calculating group-size because of their propensity to move with their mother. I grouped the observations in 5 categories: female and calves; female male and calves; female and male; female only; male only. I used only observations that included information regarding sex and age.

## 2.5 Estimation of snow depth

The snow depth was measured during the aerial count. The snow cover was measured in random chosen spots where the helicopter could land (i.e. open patches in the terrain) using a yardstick to nearest centimeter (SvenskNaturförvaltning, 2006).

## 2.6 Statistical analysis

I computed the skewness of the response variable (adult moose group-size) to measure its asymmetry (Joanes and Gill, 1998). A skewness that is different of zero results in an asymmetric distribution (Hopkins and Weeks, 1990). I obtained a positive skewness of adult moose group-size ( $\gamma = 2.2$ ). Thus, the assumption of normality was not verified in adult moose group-size. Thereby, to analyze adult moose group-size I used statistical tools that allow non-normality of the response variable.

### 2.6.1 Mann-Whitney U-tests

To test if the distributions of group-size inside and outside wolf territories were identical I used a Mann-Whitney U-test (Hollander and Wolfe, 1973). To do the same test within group categories I used a pairwise Mann-Whitney U-test with the Holm correction (Holm, 1979).

### 2.6.2 Generalized linear model

I used a generalized linear model with a Poisson distribution to model group-size as a function of the variables of interest (Zuur et al., 2009). The model can be written as :

$$Y = \theta X + \epsilon \quad (1)$$

where  $Y$  is the link function logarithm,  $X$  is a design matrix containing the explanatory variables,  $\theta$  is a vector of fixed effects parameters and  $\epsilon$  is the residual error.

I included 6 continuous explanatory variables which are moose density, wolf pack-size during the year of the survey, count of year since wolf territory was established, snow depth, latitude of observation and a spatial autocorrelation variable (Moran's Index, see section 2.6.3). I also included one categorical variable which is the moose category (see section 2.4). The variables pack-size and number of year since wolf establishment were highly correlated ( $\rho = 0.65$ , coefficient of Pearson's correlation) so both variables were not included in the same model. In order to

choose between pack-size and number of year since wolf establishment I did an univariate analysis for each variable and I selected the variable that had the lowest Akaike's information criterion (AIC) score. Pearson's correlation between other variables were all  $\leq 0.30$ .

I ran several models of different combinations of explanatory variables (see section 3.2). The model with the lowest AIC score was selected as the best model. Then to rank each model I used the AIC difference between the best model and the model  $i$  ( $\Delta_i$ ). I also computed the Akaike weight ( $\omega_i$ ) that is define as the probability of model  $i$  to be the best model among the candidate models (Burnham and Anderson, 1998). All models with  $\Delta_i \geq 10$  found no support and were not reported (Burnham and Anderson, 1998).

As defined by Burnham and Anderson (1998) the relative importance of variable  $j$  was estimated by summing the Akaike weights across all the models in the set where variable  $j$  occurs.

The goodness of fit of the best model was computed as:

$$R^2 = \frac{Deviance_{Null} - Deviance_{Best}}{Deviance_{Null}} \quad (2)$$

where  $Deviance_{Null}$  and  $Deviance_{Best}$  are the residual deviances of the model only containing the intercept and the best model, respectively (Zuur et al., 2009).

By using a Poisson distribution, I assumed that the mean of the response variable was equal to its variance (Zuur et al., 2009). Thus, to proceed to model validation I estimated the overdispersion parameter of each model (Zuur et al., 2009). In order to meet the assumption of equality between the mean of the response variable and its variance, the overdispersion parameter has to be  $\leq 1$  (Zuur et al., 2009). The models were not overdispersed since the overdispersion parameters of all models ranged 0.35 - 0.80 thus I did not have to correct for overdispersion.

### 2.6.3 Spatial autocorrelation

I tested the spatial autocorrelation of the response variable with a permutation Moran's test (Cliff and Ord, 1981). To set up the spatial weights matrix I considered two observations as neighbors if they were within 10 moose home-range distances which correspond to a distance of 16 km (Cederlund and Sand, 1994). The test showed a significant spatial autocorrelation in adult moose group-size (Moran's  $I = 0.04$ ,  $p$ -value = 0.001). Therefore to take into account and correct for spatial autocorrelation, I computed the local Moran's index (Anselin, 1995) for each observation using the same neighborhood weights matrix and included this as an explanatory variable in all the models.

### 3 Results

Moose density varied considerably within the territories with the minimum at 0.09 moose/km<sup>2</sup> in the north part of the area and the maximum at 1.88 moose/km<sup>2</sup> in the central part of the area. In the wolf territories used in the study, pack size ranged from 2-9 wolves and duration since wolf establishment ranged from 1-13 years (Appendix A).

#### 3.1 Characteristics of adult moose group-size

Of the 1335 moose observations, 383 were categorized inside wolf territories and 952 were outside (Table 1). Adult moose group size showed a right-skewed distribution (positive skewness,  $\gamma = 2.2$ ) where smaller groups were more common than larger groups (Figure 2). The medians of group-size inside and outside wolf territories were both equal to 1 but adult moose group-size inside wolf territories was significantly higher than outside wolf territories (Mann-Whitney U-test;  $W = 164052$ ,  $p$ -value = 0.0009; Figure 3). The males responded positively to the wolf presence, this was the only category that showed a significant difference in group-size between inside and outside wolf territories (Mann Whitney U-test,  $W = 4226$ ,  $p$ -value = 0.003 - Figure 4). The proportion of solitary bulls was 20% less frequent inside wolf territories than outside wolf territories (Figure 7). Group-size of the other categories were not significantly different between inside wolf territories and outside wolf territories (Mann-Whitney U-test between adult moose group-size inside and outside wolf territories for each category; Female and calves  $W = 30640$ ,  $p$ -value = 0.34; Female only  $W = 6021$ ,  $p$ -value = 0.26; Female and Male  $W = 3522$ ,  $p$ -value = 0.93; Female Male and calves  $W = 1081$ ,  $p$ -value = 0.49).

Table 1: Total number of groups observed, total number of moose and group-size range for each group category of moose in Sweden from aerial counts 2006, 2009, 2011 inside (Pres) and outside (Abs) wolf territories

Category	Female and calves		Female and Male		Female male and Calves		Female only		Male only	
	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs	Pres	Abs
<b>Wolf</b>										
<b>N Observations</b>	148	425	64	111	27	87	75	173	69	156
<b>N adult moose</b>	170	471	228	378	80	250	109	239	145	235
<b>Group-size range</b>	1-5	1-5	2-9	2-8	2-7	2-9	1-4	1-4	1-8	1-5

The mean and the median of adult moose group-size varied when each category was considered separately (Figures 4 and 5). Groups composed of adult females and males were the most gregarious category (Figures 5 and Table 1). Seventy percent of the groups including female and

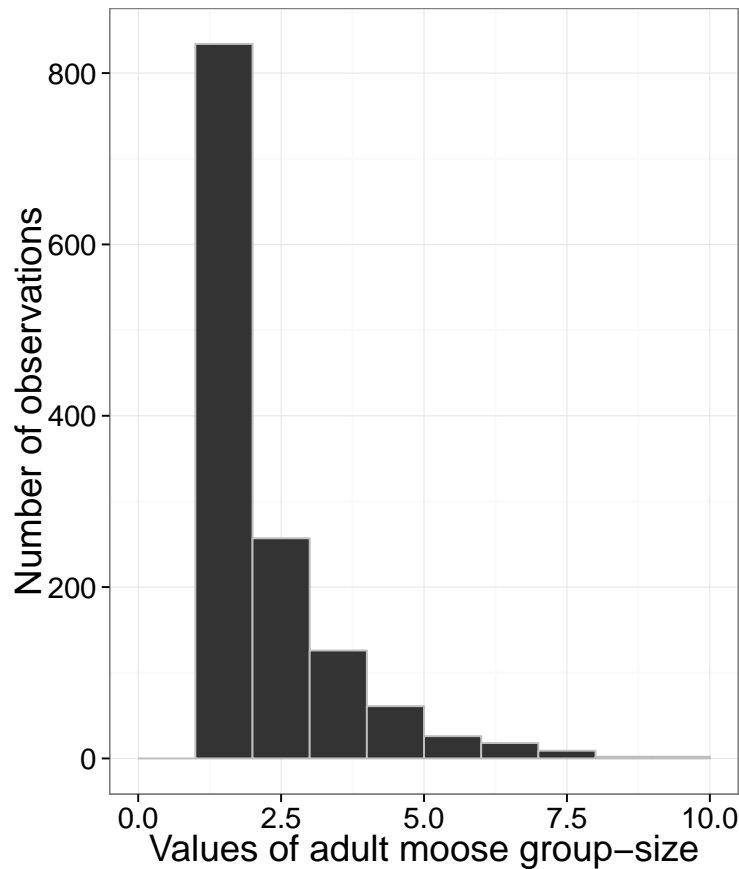


Figure 2: Right-skewed distribution of adult moose group-size ( $\gamma=2.2$ ) in Sweden from survey data collected in 2006, 2009, 2011.

male were composed of 3 or more adult moose (Figure 6). Female with calves were the most observed group category inside and outside wolf territories (Table 1) and the least gregarious category (Figures 4). Female and calves category had a minimum group-size of 1 adult and a maximum group-size of 5 adults but more than 90 % of the observations showed groups of only 1 adult female (Figure 6). In both unisex and mixed groups, the presence of calves showed a decrease in group-size compared to unisex and mixed groups without calves (Figures 4 and 5). Inside wolf territories, groups only composed of males had a significantly higher group-size than groups only composed of females (Figure 4).

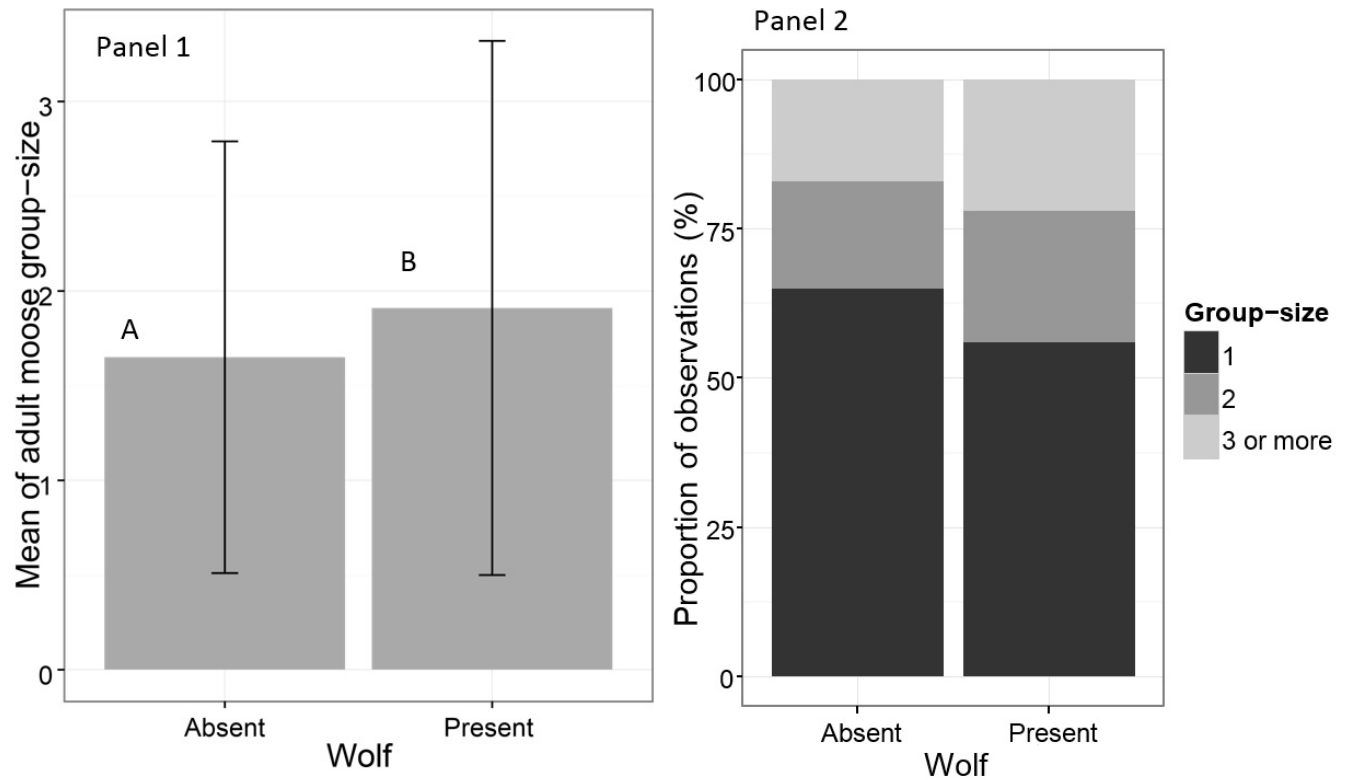


Figure 3: Characteristics of adult moose group-size in Sweden from survey data collected in 2006, 2009, 2011 inside (Present) and outside (Absent) wolf territories. Panel 1 : Mean and standard deviation. Different letters (A, B) indicates that the distribution of group-size between inside and outside wolf territories were significantly different. Panel 2 : Proportion of groups including one adult moose (dark grey), two adult moose (medium grey) and three or more adult moose (light grey). Medians are located at 50%.

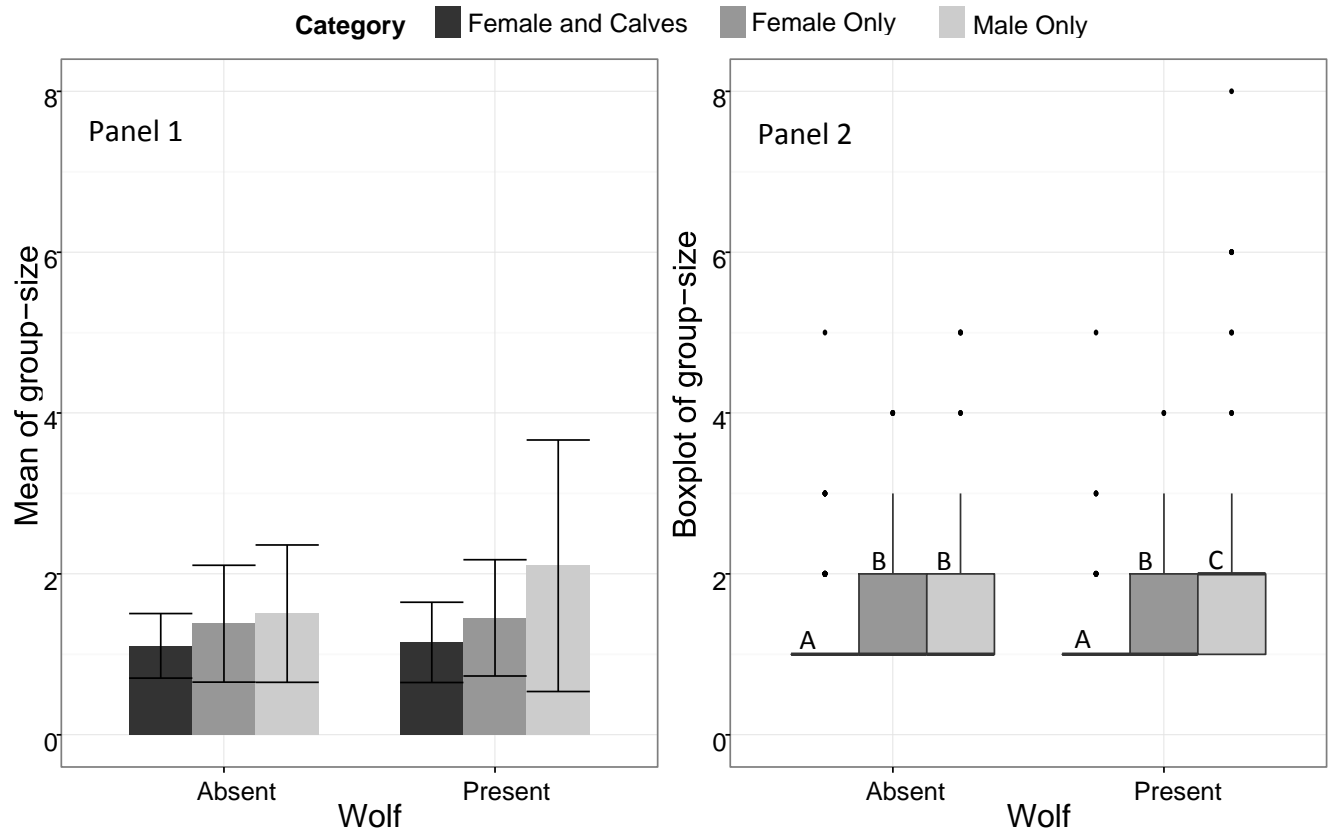


Figure 4: Characteristics of unisex adult moose groups in Sweden from survey data collected in 2006, 2009, 2011 inside (Present) and outside (Absent) wolf territories. Panel 1 : Mean and standard deviation. Panel 2 : Median (bold horizontal line), first (lower horizontal line) and third (upper horizontal line) quantiles. Dots represent outlier values. When lower and/or upper horizontal lines are not visible, it means that the first and/or the third quantiles respectively are equal to the median. Different letters (A, B or C) indicates that distribution of group-size between samples were significantly different (pairwise Mann-Whitney U-test).

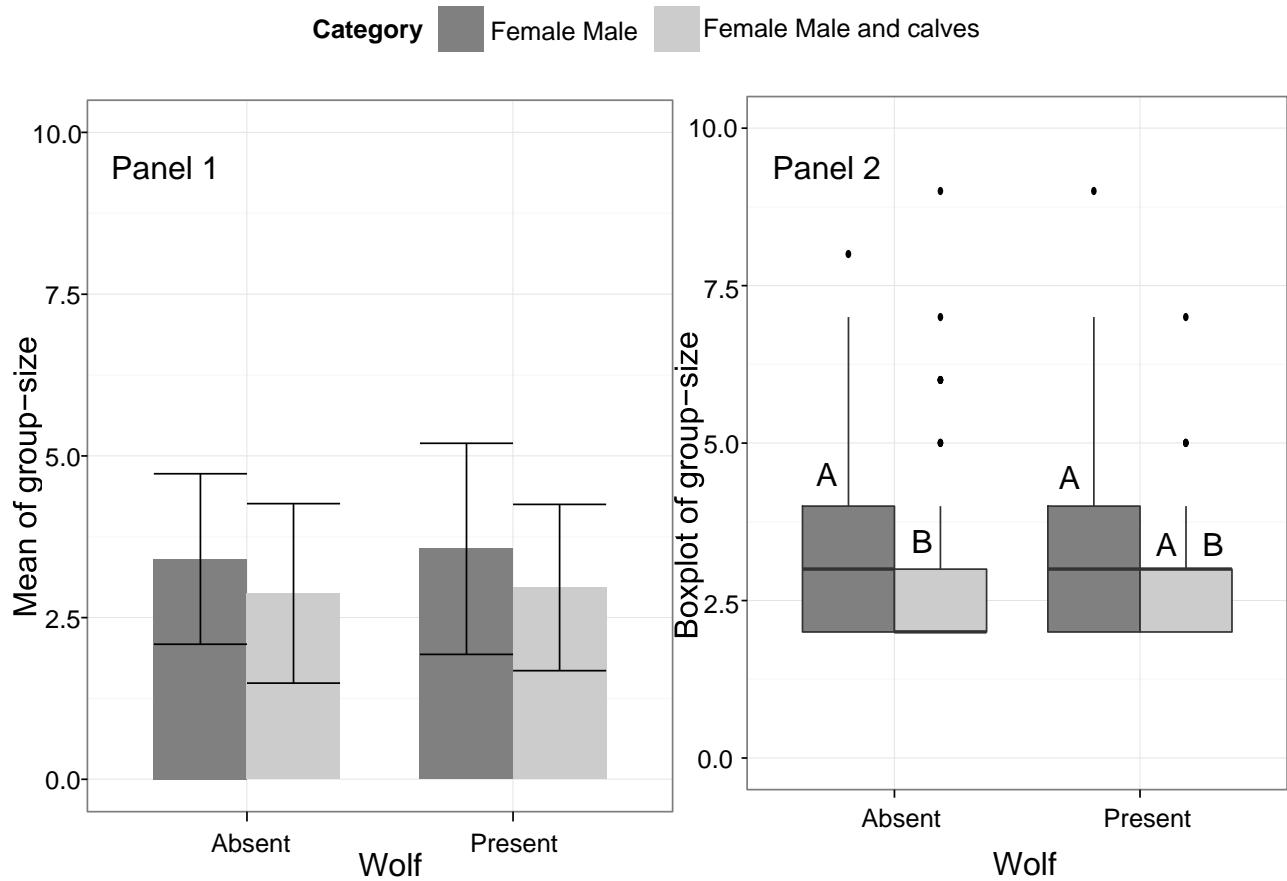


Figure 5: Characteristics of mixed adult moose groups in Sweden from survey data collected in 2006, 2009, 2011 inside (Present) and outside (Absent) wolf territories. Panel 1 : Mean and standard deviation. Panel 2 : Median (bold horizontal line), first (lower horizontal line) and third (upper horizontal line) quantiles. Dots represent outlier values. When lower and/or upper horizontal lines are not visible, it means that the first and/or the third quantiles respectively are equal to the median. Different letters (A, B) indicates that distribution of group-size between samples were significantly different (pairwise Mann-Whitney U-test).



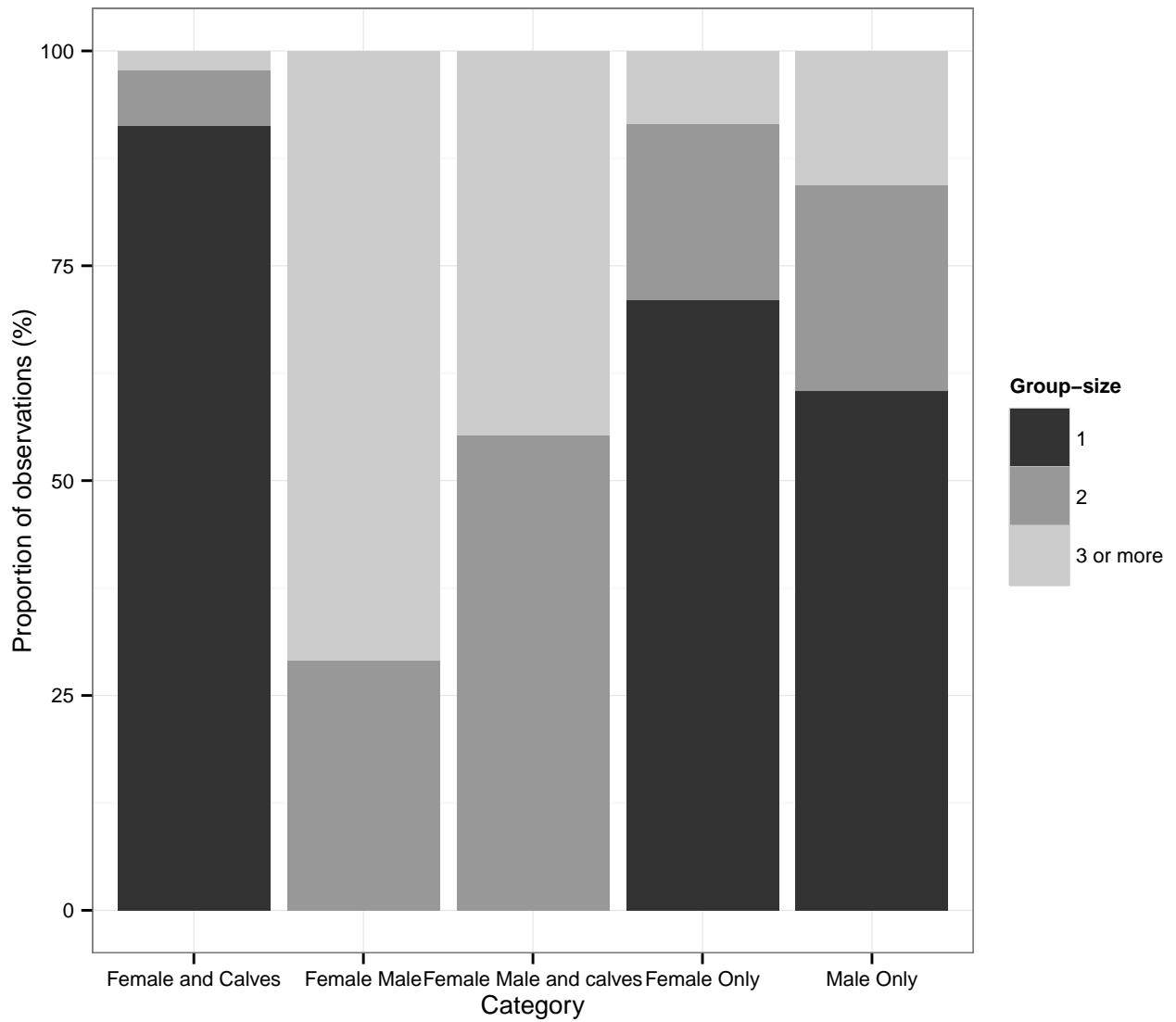


Figure 6: Proportion of groups including one adult moose (dark grey), two adult moose (medium grey) and three or more adult moose (light grey) for five group categories in Sweden from aerial counts 2006, 2009, 2011.

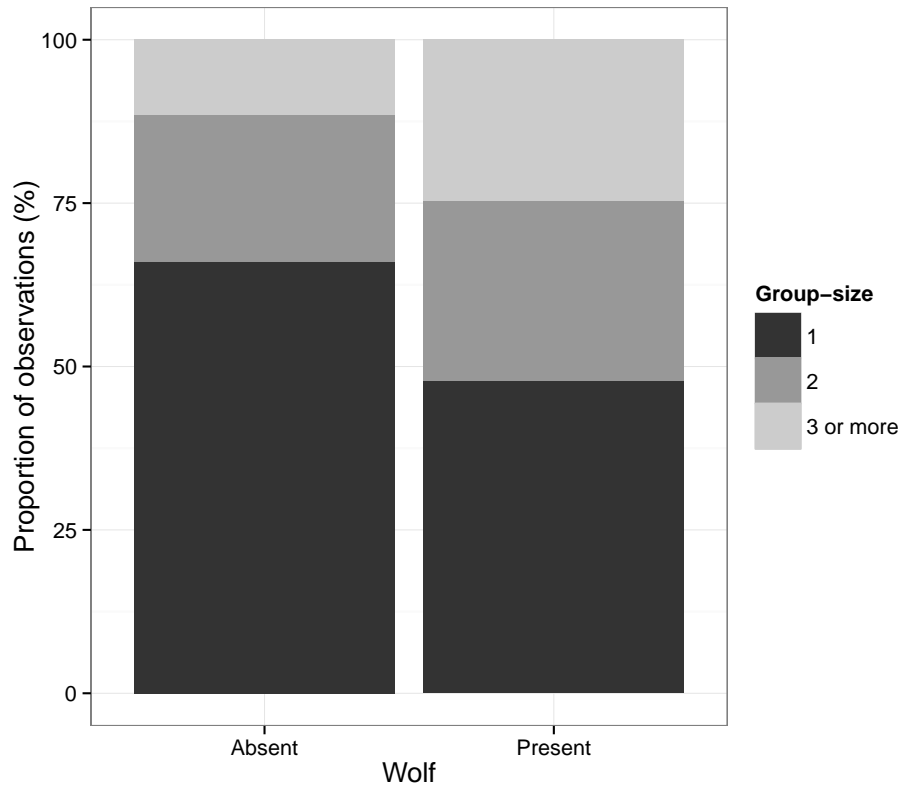


Figure 7: Proportion of Male only groups including one adult moose (dark grey), two adult moose (medium grey) and three or more adult moose (light grey) inside (Present) and outside (Absent) wolf territories in Sweden from aerial counts 2006, 2009, 2011.

### 3.2 Analysis of adult moose group-size

Pack-size and number of year since wolf establishment were highly correlated ( $\rho=0.65$ ), thus I decided to include pack-size in my model by choosing the variable with the lower AIC score. The data was spatially autocorrelated, thus a correction term was included in all models. I evaluated 8 a priori models that could explain moose grouping behaviour in Sweden, and the best model from our candidate model list included group category and snow depth (Table 2). This model explained 57% of the variation in adult moose group-size ( $R^2=0.57$ ).

Table 2: Eight best models to predict adult moose group-size in Sweden applied to 1335 moose observations from survey data collected in 2006, 2009, 2011. Models are shown in order of decreasing rank with model log-likelihood (logLik), number of model parameters (N parameters), Akaike's information criterion (AIC), AIC differences ( $\Delta_i$ ) and AIC weights ( $\omega_i$ ). All other models were  $>10\Delta_i$  from the highest ranked model.

Variable	Model	logLik	N parameters	AIC	$\Delta_i$	$\omega_i$
Group category, Snow depth	M1	-1754.97	7	3523.95	0	0.21
Group category, Moose density	M2	-1755.19	7	3524.37	0.43	0.17
Group category, Moose density, Snow depth	M3	-1754.19	8	3524.39	0.44	0.17
Group category, Snow depth, Pack-size	M4	-1754.59	8	3525.17	1.22	0.11
Group category, Moose density, Pack-size	M5	-1754.77	8	3525.53	1.58	0.10
Group category, Moose density, Snow depth, Pack-size	M6	-1753.76	9	3525.53	1.58	0.10
Group category	M7	-1756.83	6	3525.66	1.72	0.09
Group category, Moose Density, Snow depth, Pack-size, Latitude	FULL	-1753.249	10	3526.50	2.55	0.06

\*Group Category = Female and calves; Female only; Male only; Female and Male; Female Male and calves

Pack-size, moose density, snow depth and latitude were all positively correlated to adult moose group-size (Table 3). Pack-size was relatively the fourth most important variable and group category was relatively the most important variable (Table 4).

Table 3: Coefficients estimates of pack-size, moose density, snow depth and latitude to predict adult moose group-size in Sweden from aerial counts 2006, 2009, 2011

Variable	Model	Coefficient estimate
Pack-size	M4	0.0072
Moose density	M2	0.010
Snow depth	M1	0.0032
Latitude	FULL	2.3 e-07

Table 4: Relative importance of group category, moose density, snow depth, pack-size and latitude to predict adult moose group-size in Sweden from aerial counts 2006, 2009, 2011

Variable	Group Category	Moose density	Snow depth	Pack-size	Latitude
Relative importance	1.00	0.60	0.54	0.37	0.06

### 3.3 Analysis of adult male group-size

Males was the only group category that show significant difference in group size between inside and outside wolf territories. Therefore I chose to run the model selection procedure to investigate the importance of the different explanatory variables and how this is different for the male compared to the overall pattern. I ran the same analysis considering adult males group-size as the response variable. In adult male group-size analysis, I chose to include number of year since wolf establishment in my model since this variable had the lower AIC score compared to pack-size.

Similarly I validated the model by estimating the overdispersion parameter of each model which were all between 0.59 and 0.76. The best model included moose density, snow depth, number of year since wolf establishment and latitude (Table 5). This model explained little of the variation in bulls group-size ( $R^2=0.18$ ).

Table 5: Five best models to predict adult male moose group-size in Sweden applied to 225 male moose observations from survey data collected in 2006, 2009, 2011. Models are shown in order of decreasing rank with model log-likelihood (logLik), number of model parameters (N parameters), Akaike's information criterion (AIC), AIC differences ( $\Delta_i$ ) and AIC weights ( $\omega_i$ ). All other models were  $>10\Delta_i$  from the highest ranked model.

Variable	Model	logLik	N parameters	AIC	$\Delta_i$	$\omega_i$
Moose density, Snow depth, Num.year*, Latitude	FULL	-317.38	5	644.76	0	0.60
Moose density, Snow depth, Num.year*	M1	-319.72	4	647.45	2.69	0.16
Moose density, Num.year*	M2	-321.04	3	648.08	3.32	0.11
Snow depth, Num.year*	M3	-321.16	3	648.33	3.57	0.10
Num.year*	M4	-323.88	2	651.77	7.01	0.02

\*Num.Year = Number of year since wolf establishment

## 4 Discussion

I showed that wolf re-establishment in south-central Sweden did not lead to a strong change in moose grouping behaviour. Contrary to the expectation, only males significantly responded to wolf presence by forming larger groups, whereas the other categories of groups did not show a response to wolf presence. Other variables such as group category, moose density and snow depth than presence of wolf seem to be more important in explaining group-size of moose.

The intensity of the shift in grouping behaviour can be linked to the level of predation risk that each prey is subjected to. Eriksen et al. (2009) studied the frequency of encounters between wolves and moose in one wolf territory in south-central Sweden. They concluded that due to the

particularly large size of the wolf territory compared to moose home-range size, the wolves generally spent a very small proportion of their time inside the home range of each individual moose. Besides due to the really high moose density and especially the really high moose:wolf ratio in some wolf territories, the frequency of encounters between the wolves and any particular moose was very low leading to a low predation risk for individual moose since the predation pressure is spread over a high number of prey individuals (Eriksen et al., 2009). In spite of low predation risk on moose in Sweden, males, that suffer the lowest predation risk compare to female and calves, showed a response in group-size. Thus, I can assume that the absence of response from the other categories means that moose from those categories do not use group-living as an anti-predatory strategy.

A response to predation risk could be due to tradeoffs between vigilance and feeding. When choosing to reduce predation risk, animals can choose to reduce their foraging efficiency either by increasing their level of vigilance (which lead to a reduction of the time spent to feeding) or by staying in safer places where foraging efficiency quality may be lower (e.g. habitats of less forage quality or larger groups increasing intraspecific competition for resources), resulting in a reduction in body mass (Lima, 1986; Winnie and Creel, 2006). Moreover, the gain from the different behavioural strategies may be different for different categories of animals (e.g. age and sex dependence).

Since calves are the most likely preys of wolves in Sweden, moose that potentially could show a strong response are females that lose calves to wolf predation. Thus, I expected females with their calves to adopt a different grouping strategy in territories where wolf was present. This hypothesis has not been verified in this study, for which there are several reasons that could explain this observation. Dilution theory is valid if you consider a group composed of individuals under the same physical conditions which is not the case when you compare adult moose and calves. Indeed, due to their small size, calves are weaker and more vulnerable than adult moose; they are not strong competitors in group either when fleeing from wolves attack or for having access to good food quality patches (Mech and Boitani, 2003). Thus, group living may not give a strong advantage to calves. Since female aims to keep its calves alive, she may not have an advantage of being in a large group with its calves. Thus, this could explain why females with calves were solitary (females with calves were most of the time seen lonely) so they decrease their encounter rate with wolves. Additionally, females and males don't have the same body condition during winter; males still suffer from the large amount of energy consumed during rut period (Miquelle et al., 1992). Thus by being in a large group including female, males suffer higher detection rate and have a higher risk to be captured due to poor endurance during winter (Miquelle et al., 1992). Thus, the inequality of opportunity to escape may explain why moose with different body conditions do not

group as a response to wolf presence. However, considering this hypothesis, groups only composed of females should respond to wolf presence by increasing their group-size but I haven't observed this result. Since males are not the main prey of wolves, they may not suffer from higher detection rate by wolves. This can explain their decision to stay in larger group under predation risk so they can decrease their individual vigilance (group-size effect) and increase their feeding rate, especially during winter when this is the hardest foraging period of the year. Groups of females only had on average a lower group-size than males only, thus females seem to be less prone to grouping. It may be an intrinsic behaviour due to the fact that female do not group when there are with their calves (Molvar and Bowyer, 1994; Peek et al., 1974; Sweanor and Sandegren, 1986). Most observations showed that females with calves stayed solitary and avoided risky places (Molvar and Bowyer, 1994; Peek et al., 1974; Sweanor and Sandegren, 1986).

By showing in the study that more than 50% of the groups were composed of only 1 adult moose, the results support the idea that moose are not strong gregarious ungulates in Sweden. This may be linked to the high degree of aggressiveness between individuals of a same group as shown with the Alaskan moose (Molvar and Bowyer, 1994). In this survey, this aggressiveness led to a decrease in foraging efficiency. However, Miquelle et al. (1992) showed that agonistic interactions were extremely rare in Alaskan male moose. Females are more aggressive especially when they defend their young (Stephenson and Van Ballenberghe, 1995). In Sweden, female moose are also aggressive towards other moose especially when they have calves (Sweanor and Sandegren, 1986). Thus, female aggressiveness may also explain why female moose in Sweden do not form larger group in response to wolf presence. Additionally, larger group would lead to a level of antagonistic interaction between moose than would reduce benefits of being in a group.

It has been proven that snow disturbs moose movement when it is deeper than 70 cm and that they are more vulnerable to predation by wolves at snow depths greater than 75 cm (Coady, 1974; Peterson and Allen, 1974). The average snow depth in this study was 32cm and only 3% of the observations showed snow depth greater than 50cm. However, snow cover decreases food availability and creates limited and irregular food patches, thus individuals tend to stay together in areas providing high energy intake (Heard, 1992; Gude et al., 2006). In Sweden, moose foraging behaviour has been impacted as from 10 cm of snow (Mansson, 2009). I expected a positive correlation between group-size and snow depth and indeed I showed a positive effect of snow depth on moose grouping behaviour in the survey. Since snow depth in the survey was not deep enough to disturb moose movements, the positive effect of snow depth on adult moose group-size may be explained by a foraging strategy.

In my study, the latitude did not have a strong impact on adult moose group-size. Latitude could reflect factors such as variation in food abundance and variation in other ungulates density.

However, because latitude gradient did not have a great extent in the study, it is likely why it does not show any pattern to impact adult moose group-size.

I conclude that moose grouping behaviour is strongly linked to the composition of the group (sex and reproductive status (with or without calf)). These findings have implications for the future research on group living as an anti-predatory strategy in the way that the nature of the prey response to predator reintroduction is species specific and directly linked to cost-benefit trade-offs of sociality.

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## Appendix A Characteristics of wolf territories included in moose group-size survey in Sweden, 2006-2009-2011

TERRITORY NAME	MONITORING YEAR	MONITORING METHOD	NUMBER OF MONTH INCLUDED IN THE MONITORING	MONITORED HOME-RANGE SIZE (KM <sup>2</sup> )	PROPORTION ANNUAL HOME-RANGE	ESTIMATED POTENTIAL HOME-RANGE SIZE (KM <sup>2</sup> )	PACK SIZE DURING MONITORING YEAR	YEAR OF ESTABLISHMENT
KILSBERGEN	2006	GPS-collar	12	750	100%	750	8	2002
UTTERSBERG	2006	GPS-collar	12	399	100%	399	9	2004
HALGÅN	2006	VHF-collar	6	439	85%	516	5	2003
ULRIKSBERG	2006	VHF-collar	7	876	90%	973	2	2002
KLOTEN	2009	GPS-collar	12	476	100%	476	6	2007
UTTERSBERG	2009	GPS-collar	12	457	100%	457	4	2004
HEDBYN	2011	GPS-collar	12	1121	100%	1121	2	2010
LÖVSJÖN	2006	Snow tracking	6	368	-	1700	2	2005
ÄPPELBO	2006	Snow tracking	1	98	-	1700	2	2006
TENSKOG	2009	Snow tracking	3	660	-	1700	2	2007
SKRÄLLDÅLEN	2009	Snow tracking	5	938	-	1700	4	2007
SILJANSRINGEN	2009	Snow tracking	6	1627	-	1700	6	2005
LÅNGSJÖN	2009	Snow tracking	5	274	-	1700	3	2006
LOKA	2009	Snow tracking	2	366	-	1700	8	2006
HASSELFORS	2009	Snow tracking	3	125	-	1700	7	1996
AMUNGEN	2009	Snow tracking	6	895	-	1700	5	2004
FÄRNA	2011	Snow tracking	3	108	-	1700	4	2010

## Summary

Grouping behaviour by prey is commonly explained as an anti-predator strategy because of its advantages returned such as dilution effect, earlier detection of predator by prey and confusion effect of predator. Additionally, by being in group, prey may devote more time to feeding and less time to vigilance. However, as any anti-predatory strategy, group-living has a cost and requires a trade-off between the advantages given when being in group and higher attack rate due to higher detection rate from predator and sometimes higher level of competition for resources. I have been interested in studying grouping behaviour response of moose (*Alces alces*) to the reestablishment of predation pressure by wolves (*Canis lupus*) in Sweden from aerial count data collected in winters 2006, 2009 and 2011, where moose have not experienced wolf predation for 120-150 years. I predicted that group-size will change in response to wolf exposure. In a pairwise study, I tested if adult moose group-size of five categories of group (groups only composed of Female and calves; Female only; Male only; Female and Male; Female Male and calves) were different between inside wolf territories and outside wolf territories in Sweden. With a generalized linear model selection, I evaluated how predation risk is important in moose grouping formation. In addition to wolf risk, I evaluated other factors that may influence grouping behaviour such as prey density, latitude, snow depth and group composition. I showed that only males responded to wolf presence by increasing their group-size. Since males are not the main prey of wolves, they may not suffer from higher detection rate from wolves. Thus, by being in larger groups they may devote more time to feeding and less time to vigilance. On the contrary, female with calves, which are the main prey of wolves, used a different strategy and stayed solitary. Female may be intrinsically less prone to grouping. Additionally, females suffer more the costs of being in larger group than males. These findings have implications for the future research on group living as an anti-predatory strategy in the way that the nature of the prey response to predator reintroduction is species specific and directly linked to cost-benefit trade-offs associated to sociality.

## Résumé

Le choix de vie en groupe est souvent expliqué comme une stratégie d'anti-prédation par ses avantages donnés aux proies tels que l'effet dilution, une détection plus rapide du prédateur par les proies et l'effet de confusion du prédateur. De plus, en groupe les proies peuvent allouer moins de temps à la vigilance et plus de temps à l'alimentation lorsqu'elles sont en groupe. Cependant, comme toute autre stratégie d'anti-prédation, la vie en groupe a un coût et les individus faisant ce choix doivent faire un compromis entre les avantages donnés par la vie en groupe et ses désavan-

tages tel qu'un taux d'attaque plus élevé des groupes par les prédateurs et parfois un niveau plus élevé de compétition pour l'accès aux ressources. J'ai étudié le comportement d'agregation des élans (*Alces alces*) face à la ré-apparition de la pression de prédation par les loups (*Canis lupus*) en Suède à partir de données de comptage aérien fait les hivers 2006, 2009 et 2011, où la pression de prédation a été relâchée pendant 120 à 150 ans. J'avais prédit que la taille de groupe des élans serait modifiée en réponse à la présence des loups. Par une étude présence/absence, j'ai testé si la taille de groupe d'élans adultes, divisée en 5 catégories (groupes uniquement composés de: Femelles et veaux; Femelles; Males; Femelles et Males; Femelles Males et veaux), était différente entre les zones de présence et d'absence du loup en Suède. A partir d'une selection de modèles linéaires généralisés, j'ai évalué l'importance du risque de prédation dans la taille de groupe des élans. En plus du risque de prédation, j'ai également inclus d'autres facteurs qui pouvaient influencer la taille de groupe des élans tels que la composition du groupe, la densité en élan, l'épaisseur de neige et la latitude. J'ai montré que seul les males répondaient à la présence du loup en augmentant leur taille de groupe. Les males n'étant pas la proie majeure des loups, ils souffrent moins d'un taux de detection plus élevé par les loups. Ainsi, ils peuvent allouer plus de temps à l'alimentation et moins de temps à la vigilance. A l'opposé, les femelles avec leurs veaux qui sont les proies principales des loups, ont montré une stratégie différente en restant solitaire. Les femelles pourraient être intrinsèquement moins enclin à vivre en groupe. De plus, les coûts de la vie en groupe sont plus importants chez les femelles que les males. Ces résultats pourront être utilisés dans les futures questions de recherche sur la vie en groupe comme une stratégie d'anti-prédation dans le sens où la nature de la réponse de la proie à la réintroduction d'un prédateur est dépendante de l'espèce et directement liée aux compromis couts-bénéfices associés à la socialité.