

Moose (*Alces alces*) calf survival rates in the presence of wolves (*Canis lupus*) in southeast Norway

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Abstract Wolves (*Canis lupus*) are recolonizing Scandinavia and becoming a new limiting factor that should be taken into account in the management of moose (*Alces alces*). However, there is a lack of empirical estimates of moose survival after wolf recolonization. We investigated the effects of wolf abundance, moose litter size (single/twin calves), and climatic factors on annual and seasonal calf survival rates in a moose population in southeast Norway. We used data that were obtained over 7 years by radio-tracking and regular visual observations of 68 moose cows to determine the presence or absence of calves at heel. Annual and winter calf survival rates were 20–40 percentage points lower in the wolf territory compared with previous estimates of moose calf survival in similar areas that lacked wolves. Cause-specific studies of mortality would further enhance our ability to determine the relative role of various limiting factors. Our study suggests that moose managers should regulate quotas to buffer the lower survival rates after wolf recolonization.

Keywords Large carnivores · Predation · Mortality · Predator–prey interactions

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Introduction

The demography of ungulates is characterized by a high and stable survival rate for adults, but a lower and more variable survival rate for juveniles (Gaillard et al. 1998, 2000). Consequently, variation in juvenile survival is a key to understanding interannual variation in abundance. At northern latitudes, severe winter conditions increase juvenile mortality through the decreased availability of food and increased expenditure of energy (Peterson 1977). During summer, newborn calves are vulnerable to both predation and other causes of mortality (Clutton-Brock et al. 1987; Linnell et al. 1995).

After their near extermination during the nineteenth and twentieth centuries, wolves (*Canis lupus*) are now recolonizing the Scandinavian Peninsula (Wabakken et al. 2010). Moose (*Alces alces*) is the predominant prey of wolves in Southeast Scandinavia throughout the year (Sand et al. 2005, 2008). Moose calves account for 90 % of all moose killed by wolves in summer and 70 % in winter (Sand et al. 2005, 2008). Wolf–ungulate systems in Scandinavia differ from those in North America with respect to both composition and density of prey and predator, as well as the magnitude of human impact on the dynamics of the prey population (Solberg et al. 2003; Sand et al. 2005). Thus, it is crucially important to quantify the survival of moose in Scandinavia after wolf recolonization.

We estimated the variation in the annual and seasonal survival rates of moose calves in Southeast Norway during the period after wolf recolonization. The data were based on observations of 68 radio-collared moose cows and determination of the presence/absence of calves at heel. If wolf predation is a major limiting factor in the studied area, we would expect to find (1) lower rates of calf survival in the study area than in areas without wolves and (2) a negative

correlation between the survival of moose calves and the abundance of wolves. We also tested (3) whether the pattern of mortality of moose calves varied among seasons.

Material and methods

Study area

The study area is located within the boreal forest zone, mainly in the municipalities of Stor-Elvdal and Rendalen, Hedmark county, Southeast Norway (~61°N, 11°E), and has an area of 5,386 km² (minimum convex polygon of all moose positions, [Online Resource](#)). The densities of moose in Stor-Elvdal and Rendalen were relatively high, with estimated densities in the summer of ~1.1 moose per km² (Gundersen 2003). There are usually moose at all elevations in this area during summer, but they tend to migrate to lower altitudes and gather in valley bottoms (>60 % increased density) around the Glomma River as snow accumulates at higher elevations during winter (Storaas et al. 2005). The body condition of the moose in Koppang during the study period was generally high, and the level of competition for resources appeared to be low (Gundersen 2003). In the absence of predation, human harvest and collisions with vehicles have been shown to be the main causes of mortality (Gundersen 2003). In Hedmark, approximately 7,800 moose were harvested in 2007 (Statistics Norway 2008). Roe deer (*Capreolus capreolus*) (0.01 per km²) and red deer (*Cervus elaphus*) (0.1 per km²) occurred at lower densities, whereas there were no reindeer (*Rangifer tarandus*). Wolves were present in varying numbers and pack sizes during the study period (see below). There were no reproducing brown bears (*Ursus arctos*) in the area, but there were dispersing males (Bjervamoen et al. 2008). It is unlikely that bears played a major role in the system owing to their sparsity and extensive home ranges (Swenson et al. 1998).

Moose observation data

We collected data on moose calf survival from 1999 to 2005 and in 2007. We determined the presence/absence of calves of 68 radio-collared moose cows by ground tracking and visual observations during summer, and with the aid of aerial surveys during winter. We only included observations where a calf had been observed alive at the start of the time interval, and the presence/absence of the calf had to be known at the end of the time interval (i.e., year or season). When moose calves were observed alive during one sampling session but were absent during the next, and were not observed alive on later occasions, they were assumed to have died during the interval between the first two sessions.

This is a reasonable assumption because moose are typical followers with a tight bond between mother and offspring after the first week of life not included here. The proximate causes of calf deaths were unknown. Data that were affected by human hunting activity were excluded. Individual moose cows ($n=68$) were recorded between one and nine times in the data set (summer, mean=2.9, SD=2.1; winter, mean=2.4, SD=1.5; year, mean=2.6, SD=1.7). In total, the data set comprised 6 years, six winter seasons, and seven summer seasons with 157, 127, and 187 observations (i.e., survival/death of individual moose calves at the end of a season or year), respectively. Owing to the data structure, with calf presence at the start of observation and inconsistent resighting effort, we could not use the mark–resight methodology (Bonenfant et al. 2005).

Wolf data

Wolves were present in the study area from 1997 until spring 2005 ([Online Resource](#)). However, by the summer of 2005, no wolves remained in the study area. In 1999, there were two wolf territories in Stor-Elvdal and Rendalen, namely the Koppang and Atndalen territories. All wolves in the Atndalen territory, except one, were shot in February 2000. Given that none of the radio-collared moose was observed inside Atndalen, we chose not to consider this territory in the analyses. From 2000 to 2005, the Gråfjell and Koppang wolf territories co-existed, with the sizes of packs and territories changing over the years. The majority of moose positions were found inside the Koppang wolf territory, whereas only part of the Gråfjell territory overlapped with the study area.

Wolves became established in the Koppang territory in 1996 and reproduced every year from 1997 to 2000. In 1999/2000 and 2000/2001, the pack size reached its peak, with 11–12 wolves present in both years (Aronson et al. 2000; Wabakken et al. 2001). In September 2000, the alpha male was shot, after which the pack disintegrated gradually. In the winter of 2001/2002, a new male migrated into the territory, and reproduction was recorded the following summer (Wabakken et al. 2002). In 2003, no reproduction was confirmed, and only a scent-marking pair remained in the territory, and the borders of the territory expanded considerably. DNA analysis showed that these two wolves were closely related, being father and daughter. These wolves were marked with global positioning system (GPS) collars in the winter of 2003/2004. Reproduction was confirmed in 2004, but the pups left the territory in August (Wabakken et al. 2005). The remainder were shot legally in January 2005, following political decisions to exterminate wolves in the area.

The Gråfjell wolf territory was established in 2000, in parts of the municipalities of Åmot, Stor-Elvdal, and Rendalen east of the Glomma River ([Online Resource](#)). The wolves reproduced for the first time in 2001, but the pups were not seen again after November (Wabakken et al. 2002). Three pups were marked with GPS collars during these years, and they all left the territory at approximately 1 year of age. The alpha male was marked with a GPS collar in 2001, and the alpha female was first radio-collared in 2001 and then marked with a GPS collar in 2002 (Wabakken et al. 2005). During the next 3 years, the pair reproduced successfully, until the alpha female was shot in January 2005. The alpha male was found dead in June, with death estimated to have occurred in approximately mid-May.

In 2000, the Gråfjell territory overlapped almost completely with the Koppang wolf territory. During the following 2 years, there was no overlap, until expansions by the Koppang pack led to partial overlap of the territories in 2003/2004 and total overlap in 2004/2005.

The sizes of the wolf packs, pack structure, and territory borders were estimated mainly from ground tracking on snow and with the aid of radio-telemetry. Three variables that reflected wolf abundance were each tested separately in the analyses: (1) mean number of pack members per year/summer/winter multiplied by the proportion of the area of the wolf territory that overlapped with the study area during the same period for the Koppang wolf territory alone (“Koppang wolf”; continuous variable), (2) the equivalent value for the Koppang and Gråfjell wolf territories combined (“Koppang+Gråfjell wolf”; continuous variable), and (3) the size of the wolf pack in the Koppang wolf territory [“Wolf group size”; categorical variable; categories of large group (≥ 4)/small group (≤ 3)/no wolves (only in summer)].

Climate data

Data from weather stations were provided by The Norwegian Meteorological Institute. Summer climate variables included were averages of monthly mean precipitation (millimeters) and temperatures ($^{\circ}\text{C}$) in May and June. Winter climate variables included were averages of monthly mean snow depth and mean temperature ($^{\circ}\text{C}$) from December to March, and length of winter (number of days from the first day on which snow depth exceeded 30 cm until the temperature stabilized above 0°C). Owing to strong correlations between winter climate variables, the first axis (which explained 89 % of the variation) of a principal component analysis was also tested as an index of winter severity. Pearson's correlation was used to screen against collinear variables.

Statistical analysis

We analyzed survival at both annual (June–April) and seasonal (summer, June–September; winter, September–April) levels, while we compared seasonal survival rates on a monthly basis to account for the unequal number of months in each season. Moose calf survival rates were calculated as the proportion of calves that survived over a given time period. Survival rates were compared using Student's *t* test.

We tested the effects of the size of the moose litter (single or twin calf), climatic factors, and wolf abundance on moose calf survival (binomial) with generalized linear mixed models (GLMMs) using the lme4 package in the program R, version 2.13.0. All fixed factors that varied between years were entered separately, whereas we tested the additive effect of litter size and interactions of litter size and wolf abundance, and of litter size and climate. To control for potential bias owing to the different numbers of days between the first and last observation, we entered length of observation period as a covariate to the best models. This is slightly problematic for the winter season, because an absence of calves at an early observation often led to further observations being cancelled. To control for repeated sampling within years and of the same moose cows across years, year and moose cow ID were included as random variables. Akaike's Information Criterion (Burnham and Anderson 2002) was used for model selection.

Results

Annual survival rates for moose calves in the study area ranged from 0.56 to 0.76 between years, whereas winter survival rates ranged from 0.62 to 0.92 and summer survival rates from 0.87 to 1. Mean monthly survival rates for the calves did not differ significantly between summer (mean = 0.98, SD = 0.01) and winter (mean = 0.96, SD = 0.02).

Among the selected models ($\Delta\text{AIC} \leq 2$), wolf abundance was related negatively to annual and winter calf survival rates (Table 1). Furthermore, there was a negative correlation between litter size and calf survival over winter (Table 1). Inclusion of length of observation period did not affect these patterns. The most parsimonious model of annual calf survival included wolf group size alone, with lower survival in years with a large group of wolves (Table 1, Fig. 1a). In addition, a model that included the interaction between litter size and wolf group size, with lower survival of twin calves than of single calves, performed relatively well (Table 1). In winter, the two best models included (1) litter size and winter temperature and (2) wolf group size and litter size, with lower survival for twin calves than for single calves as well as lower survival in years with large wolf groups (Table 1, Fig. 1b). For summer, the best model included the interaction of wolf group

Table 1 Estimates from the best models to explain annual and seasonal moose calf survival rates

Model	AIC	Δ AIC	α	B_1 (SE)	p value	B_2 (SE)	p value	B_3 (SE)	p value	B_4 (SE)	p value
Annual survival											
$\alpha+B_1$ (wolf group size ^b)	201.3	0.0	0.36	0.74 (0.3)	0.03	–	–	–	–	–	–
$\alpha+B_1$ (twin)+ B_2 (wolf group size ^b)+ B_3 (twin \times wolf group size ^b)	201.4	0.1	0.61	-1.13 (0.6)	0.05	0.44 (0.4)	0.28	1.28 (0.8)	0.11	–	–
$\alpha+B_1$ (twin)+ B_2 (wolf group size ^b)	202	0.7	0.46	-0.45 (0.4)	0.25	0.79 (0.4)	0.03	–	–	–	–
Winter survival											
$\alpha+B_1$ (twin)+ B_2 (winter temperature)	132.8	0.0	10.4	-1.23 (0.6)	0.05	1.23 (0.4)	<0.01	–	–	–	–
$\alpha+B_1$ (twin)+ B_2 (wolf group size ^b)	132.9	0.1	0.99	-1.55 (0.6)	0.02	2.18 (0.6)	<0.01	–	–	–	–
$\alpha+B_1$ (twin)+ B_2 (winter temperature)+ B_3 (twin \times winter temperature)	134.3	1.5	9.23	2.82 (5.8)	0.63	1.06 (0.4)	0.01	0.59 (0.8)	0.48	–	–
Summer survival											
$\alpha+B_1$ (twin)+ B_2 (wolf group size ^b)+ B_3 (observation length) + B_4 (twin \times wolf group size ^b)	107.7	0.0	13.0	-2.1 (1.2)	0.08	-0.74 (1.6) ^c	0.64	-0.09 (0.1)	0.09	1.46 (1.9) ^c	0.46
$\alpha+B_1$ (twin)+ B_2 (wolf group size ^b)+ B_3 (twin \times wolf group size ^b)	108.9	1.2	3.9	-2.1 (1.2)	0.08	-2.24 (1.1) ^d	0.04	1.58 (1.9) ^c	0.41	19.9 (>100) ^d	0.99
$\alpha+B_1$ (Koppang wolf)	110.0	2.3	2.05	0.14 (0.1)	0.17	-1.97 (1.1) ^d	0.07	18.8 (>100) ^d	0.99	–	–

All models are GLMMs with moose cow ID and year as random variables

^a Twin; reference= single calf

^b Wolf group size; reference= large wolf group

^c No wolves (only in summer)

^d Small wolf group

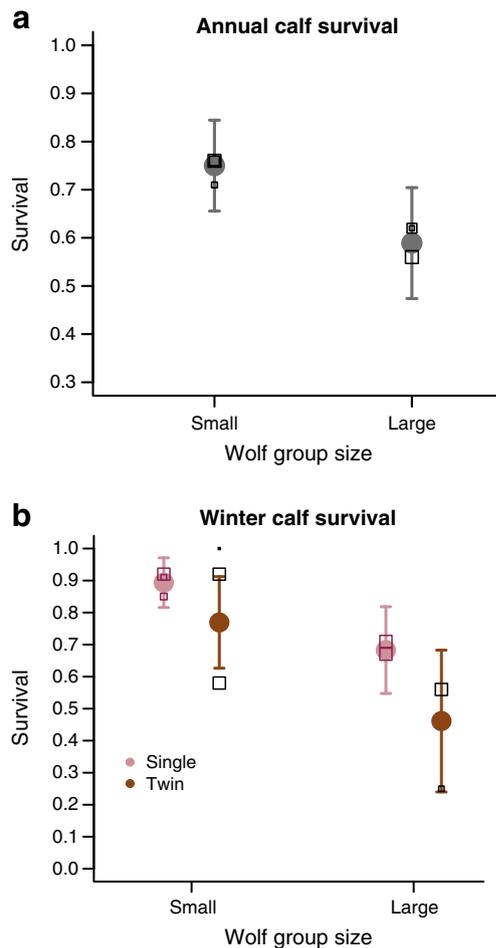


Fig. 1 Predicted means and 95 % CI for moose calf survival in relation to wolf group size in the Koppang wolf territory based on generalized linear models of calf survival; **a** Annual survival~wolf group, $N=157$ and **b** winter survival~twin+wolf group, $N=127$. Squares represent observed survival rates for a given year, with sizes of the squares reflecting relative sample sizes

size with litter size and accounted for the number of days of observation. However, the only significant parameter suggested lower (rather than higher) survival specifically for singleton calves during years of small compared with large wolf group size, providing no clear biological inference.

Discussion

Recolonization by wolf populations in Scandinavia is a major challenge for the management of ungulates (Nilsen et al. 2005), because wolves are a new and potentially important limiting factor in the system. To facilitate harvest management, it is crucial to assess moose survival after wolves have become established. A previous study reported high estimates of moose calf survival in the south of Norway in areas that

lacked large carnivores (Saether et al. 1996), whereas our estimates of annual survival rates for moose calves were 20 to 40 percentage points lower. Thus, our study supports prediction (1), namely that moose survival is lower after wolf recolonization. We could not establish directly from our data that the reduction in survival was due to wolf predation; however, the significant negative effects of wolf abundance on annual and winter survival for moose calves supported such an interpretation, in agreement with prediction (2).

Wolf predation is commonly reported to act as an additive mortality factor when the abundance of prey is below the nutrient–climate ceiling, that is, below the carrying capacity of the range (Theberge 1990; Gasaway et al. 1992). Given that the moose population in Koppang was not considered to be limited by food (Gundersen 2003), the main effect of wolf predation was expected to be additive. However, we found some indication for a negative effect of litter size on calf survival, which suggested an element of compensation. In general, twin calves are smaller than singletons, and it is also likely that small calves will be more vulnerable to other causes of mortality besides predation. This suggests indirectly that the age and experience of a mother are less important than calf size for calf survival, because young females rarely produce more than a single calf (Saether and Haagenrud 1983). Before the reestablishment of wolves, hunting and collisions with vehicles were the main causes of moose mortality in the study area (Gundersen 2003). The negative effect of winter temperature on calf survival might partly reflect the increase in the rate of vehicle collisions that occurs during harsh winter climate (Gundersen 2003). However, the average monthly survival rates were equal in summer and winter, and we cannot rule out that wolves affected calf survival in both seasons, although the effect of wolf abundance was not significant during summer. The lack of a significant effect of wolf abundance on calf survival rates in summer might have resulted from smaller differences in predation rates between wolf groups in summer or from a possible masking of the influence of wolf predation by brown bear predation. Our predicted values for summer survival might be overestimations, given that radio-tracking of moose cows during summer typically started in late May or early June; this may have resulted in some cases of mortality being missed before the observations were initiated.

The results of the study suggest that the reestablishment of wolves in Scandinavia might reduce moose calf survival in a manner that depends on wolf pack size. Although the present results do not establish definitively that wolves were the proximate cause of increased moose mortality, we urge moose managers to take into consideration the reduced survival rates when setting quotas to avoid decreases in the population size of moose. This will probably become increasingly important if the size of wolf populations is allowed to increase.

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