Three approaches to estimate wolf Canis lupus predation rates on moose Alces alces populations

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Abstract We employed three different methods to estimate predation rates on moose in a newly colonized wolf territory in Norway. In the first two methods, we estimated predation rates based on the difference in calf/cow ratios outside and inside the wolf pack territory from (1) hunter observations and (2) aerial surveys. In the last method, (3) we estimated loss of calves of radio-collared cows inside and outside the wolf pack territory. The difference in mortality rates estimated between the area subject to predation and the area outside the wolf pack territory essentially constitutes the additive component of predation. We also tested the sensitivity of violating the assumptions of methods 1 and 2 related to equal fecundity and mortality because of other factors than predation inside and outside the wolf pack territory. Predation rates varied considerably between years and methods used, with hunter observations (method 1) giving the lowest and aerial surveys (method 2) giving the highest estimates. Method 3 (radio telemetry) was the most direct assessment of predation and probably the best approach to estimate predation rates in moose. However, all three methods show the same yearly changes and may therefore be appropriate to question trends trough time or between areas.

Keywords Aerial survey . Hunter observations . Management . Predator–prey interaction . Radio telemetry

Introduction

Ungulate population dynamics have been explained by density-dependent food limitation, environmental stochasticity (Sæther 1997; Gaillard et al. 1998), and by human exploitation (Renecker and Hudson 1991). In areas with large carnivores, predation may be important for the development of ungulate populations (Gasaway et al. 1992; Van Ballenberghe and Ballard 1994; Messier 1994; Ballard and Van Ballenberghe 1997; Hayes and Harestad 2000), although the impact of predation has proven difficult to determine. Studies of wolf (Canis lupus) interactions with their prey (e.g., Boutin 1992) have generated much controversy regarding the relative impact of wolf predation on the dynamics of northern ungulate populations (Boutin 1992; Messier 1994; Orians et al. 1997).

The present knowledge of wolf predation on ungulates comes mainly from studies of wolf predation on moose (Alces alces) in North America (see Ballard and Van Ballenberghe 1998). Wolf predation has been suggested to range from a minor (e.g., Ballard et al. 1987) to a major (Boutin 1992; Ballard and Van Ballenberghe 1998) factor limiting the growth rate of moose populations. This may reflect real variation among areas and years because of moose density (e.g., Messier 1994), wolf pack size (Hayes et al. 2000), wolf/moose ratios (Vucetich et al. 2002), prey age structure (Peterson et al. 1984; Ballard et al. 1987), and variability in other prey species (Messier and Crête 1985), but it may also be a result of the various methods employed (Boutin 1992). In most studies, the annual predation rate of wolf on moose (number of moose killed by wolf/moose population abundance) has been estimated by extrapolating the kill rates on moose (e.g., moose killed per wolf/day) observed from aircraft during winter (Boutin 1992; Ballard and Van Ballenberghe 1998). An alternative method to estimate the impact of wolves on moose populations is by monitoring radio-collared moose (Ballard and Van Ballenberghe 1998). In this approach, the losses of moose to wolf predation can be estimated directly.

On the Scandinavian Peninsula, wolves were widely distributed and relatively common until about 100 years ago. During the last century, wolves were almost eradicated by humans (Arnesson-Westerdahl 1987; Bjärvall 1988; Wabakken et al. 2001). Simultaneously, there was a significant decrease in the density of brown bears in Sweden (Swenson et al. 1994) and an almost complete extirpation of the species in Norway (Swenson et al. 1995). During the second half of the last century, predation on moose by large carnivores was therefore low in Norway and most of Sweden. This and several other factors subsequently resulted in a dramatic increase in the moose population in Fennoscandia (e.g., Cederlund and Markgren 1987; Østgård 1987; Solberg et al. 1997). During the last two decades, moose populations have been at an all time high of about one moose per km2 on the Scandinavian peninsula (Lavsund et al., unpublished data). Consequently, human harvesting has developed into a regionally important economic and recreational factor (Storaas et al. 2001) and has become the main limiting and regulating factor of moose (e.g., Solberg et al. 1999).

During the last two decades, wolves have recolonized southern parts of Scandinavia and, although still in low numbers (98–114 individuals in Scandinavia during the winter of 2001/2002; Wabakken et al. 2002), may contribute substantially to local moose mortality. Their impact
remains unknown but could potentially deviate from the North American situation because of differences in the composition of the prey and predator base, the presence of inexperienced (naïve) prey (Berger et al. 2001), differences in wolf densities (i.e., wolf pack size/territory size), and the extent of human control of the landscape.

Our work was undertaken to evaluate different methods for estimating predation rates and to provide insights into wolf predation on moose in an area recently colonized by wolves in Scandinavia. We estimated predation rates using three different approaches and datasets: (1) calf/cow ratios (CCs) as recorded by moose hunters in September–October, (2) CCs estimated from aerial surveys in December, and (3) calf survival estimated from observations of radio-collared moose cows and their calves throughout the year. We compared the results of the three approaches and evaluated the sensitivity of violating inherent assumptions.

Materials and methods

Landscape description

The study area was located in a boreal ecosystem near Koppang in Stor-Elvdal and Rendalen municipalities, SE Norway (~61°N, 11°E; Fig. 1). The winter typically starts in October and ends in late April. Snow covers most of the area 5 to 6 months each year. The vegetation in the area was composed of stands of Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies L.), as well as scattered boreal deciduous species, such as birch (Betula pubescens), willow (Salix spp.), mountain ash (Sorbus aucuparia), aspen (Populus tremula), and hoary alder (Alnus incana). The Glomma River runs along Østerdalen, the main valley in the area (Fig. 1). Most of the study area ranges between 300 and 700 m but also includes smaller alpine areas up to about 950 m. The area could best be characterized as semiwilderness, with low human population density (<1.0 inhabitant per km2) including extensive forestry and a high density of gravel forest roads (approximately 1 km of road per km2).

The moose population

Moose in the study area occur at relatively high densities (Fig. 2a). In summer, moose are relatively evenly distributed over the area (approximately 1.1 moose per km2 in summer; Gundersen 2003), but during winter, they aggregate in valley bottoms and lower elevations characterized by less snow (Gundersen et al. 1998). Mean home range sizes (95% kernels, Silverman 1986) of moose in the area is approximately 8 km2 (Odden et al. 1996) but varies considerable between individuals and years (mean ranges 10–30, Odden et al. 1996) and less between sex and season as is found elsewhere (e.g., Cederlund and Okarma 1988).

Until recently, there were only two major mortality factors affecting this moose population: hunting and vehicle collisions (Gundersen 2003). In 1997, a wolf pack established a territory within parts of the winter range of moose in the area (Wabakken et al. 2001, 2002). No brown bear are known to be resident in the area, although transient individuals may appear (Swenson et al. 1995). We assumed that the impact of brown bear on the moose population during our study was negligible. Similarly, we assumed predation by lynx (Lynx lynx) on moose, documented rarely in the literature (Jedrzejewski et al. 1993; Okarm et al. 1995), was not an important mortality factor.

The Koppang wolf pack

Since its appearance in the area, the Koppang wolf pack has been monitored yearly by the National surveillance program of large carnivores during winter to estimate pack size, pack structure, and territory borders (Wabakken et al. 2002). On average, 219 km (SD=49) of snow tracking where performed each winter during 57 days (SD=14) with optimal tracking conditions. Because pack size was determined by snow tracking during winter, estimates may not be representative of the pack size throughout the year (from one breeding season to the next).

From a breeding pair in the winter of 1996/1997 and reproducing all years 1997/2000, the pack increased to five in 1997/1998, seven in 1998/1999, and 11 in 1999/2000. During the 2000/2001 winter, there were still 11 individuals, but the alpha male had been removed by authorities to reduce predation on domestic sheep. The winter after the removal of the alpha male, there were only two wolves remaining in the territory the winter of 2001/2002, the alpha female and a newly immigrated male (Wabakken et al. 2002).

The wolf winter territory boundaries were estimated as the minimum convex polygon (Dalke and Sime 1938) from the outermost locations of scent marks by the breeding pair (Peters and Mech 1975; Wabakken et al. 2001). Wolf pack sizes were estimated by repeated counts from snow tracking. The pack territory was bordered
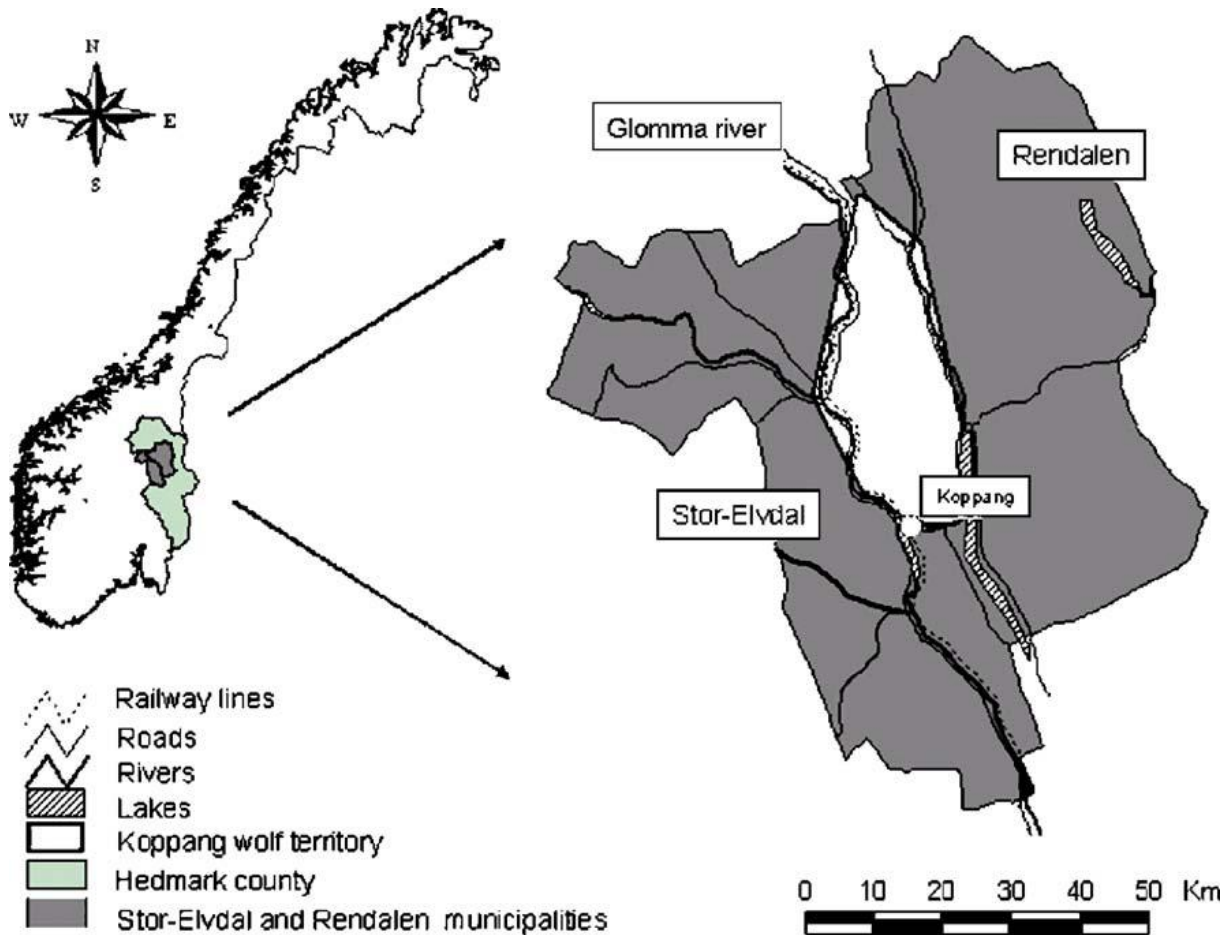
Fig. 1 The study area in south east Norway showing the two municipalities, Stor-Elvdal and Rendalen, and the wolf territory surrounded by traffic arteries

to the west by the Glomma river and the main traffic arteries at the bottom of the Østerdalen valley and was relatively stable all the years the wolf pack was present (Wabakken et al. 2002; Fig. 1). Main roads also defined the southern, eastern, and part of the northern boundary of the pack territory. The total area of the wolf territory used was 600 km2. For simplicity, the area inside the wolf pack territory was henceforth referenced as "inside" and the part of the Stor-Elvdal municipality that is not influenced by wolf predation was referenced as "outside" (Fig. 1). The size of the area referenced as "outside" was about 1,800 km2. Adjacent to the defined study area, two other wolf territories bordered the Koppang territory during parts of the study period: the Atndal wolf territory (1998/1999– 2000/2001) at the northwestern edge and the Gråfjell territory (2000/2001–2001/2002) at the southeastern edge of the Koppang territory, respectively (Wabakken et al. 2002). These areas, occupied by the Atndalen and Gråfjell packs, were excluded from the analysis (see below).

Both roe deer and red deer exist at low densities in the study area (i.e., less than 0.05 individual per km2) but did not constitute a significant part of the wolf diet (Sand et al. 2005).
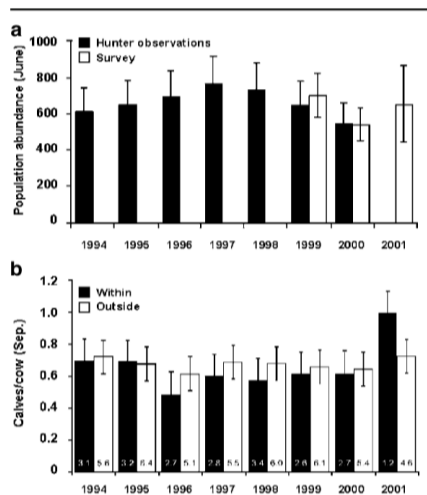
Fig. 2 a Population abundances (±2 SE) at Koppang during the period from 1994 to 2001. From 1994 to 2000, the abundance was estimated from the annual moose observation inventory. Because of low hunting effort, we have no estimates of population abundance from hunter observations in 2001. For the last 3 years, we present abundance estimates based on mark–resight methods from aerial surveys (see Gundersen 2003 for details). b Calf/cow ratios in September based on hunter observations outside and inside the wolf pack territory. Numbers inside columns are the total number of hunter days (×1,000)

Background data

Hunting statistics
Moose hunting occurred both inside and outside the wolf territory. The harvest season lasted from 25th of September until the end of October. Information on moose population structure was obtained by using indices derived from the annual moose observation inventory (Fig. 2b). The inventory is a systematic recording of sex and age (calf or older) of moose observed by moose hunters during the hunting season. All hunter observations are pooled within management units (on average about 140 km$_2$ each). The number of management units was 7 inside and 12 outside the wolf territory.

Aerial surveys
During the three winters from 1999/2000 to 2001/2002, we used mark–resight techniques from aerial surveys to estimate moose population density and structure inside and outside the wolf pack territory. All surveys were performed during a few days in December–January. Four, seven, and five independent surveys inside and two, four, and two independent surveys outside the wolf pack territory were conducted for the 3 years, respectively. Aerial surveys were subsamples of the study area flown close enough together in time to avoid duplicate counting because of moose movements. Aerial surveys outside did not overlap other known wolf packs. We classified individuals as calves, bulls, or cows and noted whether they were radio collared or not.

Radio telemetry
Since February 1999, we have radio collared a total of 121 moose (82% females) in the study area (60 in 1999, 23 in 2000, and 38 in 2001). Of these, 82 were collared inside the wolf pack territory (48 in 1999, 16 in 2000, and 18 in 2001). No calves were radio-collared, but seven females and two males were radio collared as yearlings. All moose were captured by darting from a helicopter (Arnemo et al. 2003). Radio-marked moose were relocated regularly eight to nine times a year by fixed-wing aircraft and by ground telemetry to determine movements and mortality rates.

Estimating predation rates

Approach 1—calf/cow ratios based on hunter observations
In this approach, we estimated the average (CC) observed by hunters outside $^{(CC_S^{out})}$ and inside $^{(CC_S^{in})}$ the wolf pack territory in September (S). We assumed (1) equal fecundity outside and inside the wolf territory (i.e., equal calf [Ca]/ cow [Co] ratios at parturition in June [J]) and (2) equal mortality rates from unknown factors outside and inside the wolf territory. We estimated calf/cow ratios outside (Eq. 1) and inside (Eq. 2) the wolf territory in September as:

$$CC_S^{out} = \frac{Ca_J}{Co_J} \times \frac{(1 - m_{Ca,u})}{(1 - m_{Co,u})}, \text{ and} \qquad (1)$$

$$CC_S^{in} = \frac{Ca_J}{Co_J} \times \frac{(1 - m_{Ca,u})}{(1 - m_{Co,u})} \times \frac{(1 - m_{Ca,p})}{(1 - m_{Co,p})}, \qquad (2)$$

where m is the calf- or cow-specific mortality rate because of unknown factors (u) and predation by wolf (p). Hence, $(1-m_{i,j})$ denotes survival rates for moose category i, given mortality factor j. Assuming (3) no predation of cows:

$$CC_S^{in} = CC_S^{out}(1 - m_{Ca,p}), \qquad (3)$$

which may be solved to estimate the mortality rate of calves because of predation as:

$$m_{Ca,p} = 1 - \frac{CC_S^{in}}{CC_S^{out}}. \qquad (4)$$

Approach 2—calf/cow ratios based on aerial surveys
As in approach 1, we used the difference between CCs outside and inside the wolf pack territory to estimate calf predation rates. Aerial surveys were mainly performed in December–January (D), approximately 7 months after calving.

Because CCs $(CC_D^{out}$ and $CC_D^{in})$ were estimated after the hunting season (September–October), Eqs. 1 and 2 have to be expanded to include survival given harvest mortality (h) for calves and cows, respectively: $(1-m_{i,h})$. Because of predation, some hunters have changed their harvest strategies inside the wolf territory. Hence, harvest mortality differs between the two areas. CCs outside and inside the wolf territory were estimated as:

$$CC_D^{out} = \frac{Ca_J}{Co_J} \times \frac{(1 - m_{Ca,u})}{(1 - m_{Co,u})} \times \frac{\left(1 - m_{Ca,h}^{out}\right)}{\left(1 - m_{Co,h}^{out}\right)}, \text{ and} \qquad (5)$$

$$CC_D^{in} = \frac{Ca_J}{Co_J} \times \frac{(1 - m_{Ca,u})}{(1 - m_{Co,u})} \times \frac{\left(1 - m_{Ca,h}^{in}\right)}{\left(1 - m_{Co,h}^{in}\right)}$$
$$\times \frac{(1 - m_{Ca,p})}{(1 - m_{Co,p})}. \qquad (6)$$

Equation 5 may be solved with regard to Ca_J/Co_J to estimate the mortality rate of calves because of predation as:

$$m_{Ca,p} = 1 - \frac{CC_D^{in}}{CC_D^{out} \times \frac{\left(1 - m_{Co,h}^{out}\right)}{\left(1 - m_{Ca,h}^{out}\right)} \times \frac{\left(1 - m_{Ca,h}^{in}\right)}{\left(1 - m_{Co,h}^{in}\right)}}. \qquad (7)$$

This approach assumes no predation of cows. The denominator reflects the number of calves per cow available for predation after adjusting for mortality because of unknown factors and harvest.
Gundersen (2003) estimated harvest rates for calves and cows inside the wolf territory by dividing the known number of hunted animals by the number of animals in June. We do not have any good estimates of harvest rates outside the wolf territory. Harvest rates outside the wolf territory were thus set to be the average estimated harvest rates inside during the years 1994/1999 (i.e., before harvest changed because of predation), whereas we used the yearspecific estimates of harvest rates inside.

Approach 3—calf mortality based on radio telemetry

We estimated calf predation rate by comparing survival of calves of collared moose cows outside and inside the wolf territory during the period 1999/2000 through 2001/2002. To avoid the possible confounding effect of moose cows moving in and out of the wolf territory, we used only data from females that were exclusively resident either outside or inside the territory. Calves known to be dead from hunting were excluded from the analyses. A total of 65 cows, reflecting 85 cow years, were included in the analyses (18 cows outside and 47 inside). Calf predation rate for the 11-month period from June to April was estimated as:

$$m_{Ca,p} = 1 - \frac{S^{in}}{S^{out}}, \qquad (8)$$

where S^{out} and S^{in} represent calf survival outside and inside the wolf territory, respectively. Calf survival was estimated as the proportion of calves known to be present in June still alive in April. We assumed that calf

mortality outside the wolf territory was due to unknown factors and that this resembles unknown mortality inside the wolf territory.

To compare predation rate estimates among the various approaches, we rescaled all estimates to a monthly basis. The different approaches all depended on the common assumption of equal predation throughout the year (Boutin 1992; Ballard and Van Ballenberghe 1998).

Estimating annual number of kills

Predation rates are dependent on prey population size and should decrease with moose density (Messier 1994). To make our results comparable with other studies, we estimated the total number of moose killed (K_{Tot}) by wolves each year as:

$$K_{Tot} = K_{Ca} + K_Y + K_{Co} + K_B \qquad (9)$$

where K_{Ca}, K_Y, K_{Co}, and K_B are the number of calves, yearlings, adult cows, and bulls killed, respectively. Data based on snow-tracking wolves in the Koppang wolf territory during the winters from1997/1998 through 2001/2002, a total of 1,450 km of wolf trails, indicated that 63% of all kills were calves (n=19), 27% yearlings (n=8), and 10% adult cows (n=3; Wabakken, unpublished data). No adult bulls have been confirmed killed by wolves inside the territory (i.e., K_B=0). Assuming constant sex and age structure of the population, we have:

$$K_Y = \frac{8}{19} K_{Ca} \text{ and} \qquad (10)$$

$$K_{Co} = \frac{3}{19} K_{Ca}. \qquad (11)$$

We estimated K_{Ca} by multiplying the estimated number of calves inside the wolf territory in June by the estimated annual predation rates. Estimates of moose population size and composition in June were obtained from Gundersen (2003).

Analyzing assumptions

Equal fecundity outside and inside
Equal fecundity outside and inside the wolf territory is common to approaches 1 and 2. We have no evidence that habitat quality or other environmental variables affecting fecundity differ between the two areas. However, as wolves primarily prey on calves and yearlings, recruitment of cows inside the wolf territory would decrease. This, in combination with lower hunting activity during the last years, suggests that the average age of cows was higher inside than outside the wolf territory in recent years. Because prime-age cows are more fecund (Ericsson et al. 2001; Gundersen 2003), this may yield a higher calf/cow ratio inside than outside the wolf territory. Females inside whose calves are predated in early summer may also experience increased fecundity because of enhanced body condition the next year (see Swenson et al. 2001). Higher fecundity inside than outside the wolf territory would cause an underestimation of predation rates in approach 1 and 2, and may result in $(CC_S^{out}) < (CC_S^{in})$, which would yield biased estimates of predation rates.

Equal mortality rates from unknown causes
Equal mortality rates from unknown causes outside and inside the wolf territory is assumed in all three approaches. Mortality because of disease or accidents such as drowning are generally rare in Norway (Sæther et al. 1996; Stubsjøen et al. 2000; Gundersen 2003) and is not expected to differ between the two areas. Mortality rates because of vehicle accidents are similar for all age and sex classes of moose in our area (Gundersen 2003) and should not affect the CC differently between the two areas in approaches 1 and 2. In approach 3, we do not know the source of calf mortality. Estimated predation rates in approach 3 may be either overestimated (higher mortality inside than outside) or underestimated (higher mortality outside than inside) if mortality rates varied between the two areas. However, there is no reason to believe that loss of calves from collared cows because of collisions with vehicles differed between the two areas because all collared cows live in areas associated with main traffic arteries (Hedmark University College, unpublished data).

No cow predation
No predation of cows is an inherent assumption to all approaches. Certainly, there is some predation of cows (see above). The consequence of violating this assumption would be that predation rates would be underestimated in approaches 1 and 2.

Evaluating violation of assumptions

Besides sampling errors our analytical approaches should be sound when fecundity and all mortality except for predation of calves is equal outside and inside the wolf territory and differences in harvest rates are taken into account. If mortality rates differ between the two areas, our estimates should still be unbiased if varying rates of mortality do not affect CCs. We evaluated the magnitude of bias in the estimated predation rate because of violation of assumptions using simulations. We compared a true predation rate of calves (M_p) with an estimated rate (m_p). Bias was defined as the percentage discrepancy from the true value:

$$\text{bias} = \left| \frac{M_p - m_p}{M_p} \right| \times 100. \qquad (12)$$

We used the same number of calves and cows per 100 km2 in June outside and inside a hypothetical predation area as initial values in the simulations (45.0 cows and 35.6 calves [i.e., a CC equal to the fecundity rate of 0.79]; Gundersen 2003). We chose a high and a low value (0.4 and 0.05, respectively) for the true annual predation rate on calves. True predation rates were then transformed to yield predation rates for a 4-, 7-, and 11-month period, corresponding to approaches 1, 2 and 3, respectively. We measured the sensitivity of the assumptions by:
1. Changing the fecundity by increasing the number of calves in June, either outside or inside, by up to 100%, in increments of 10%. This was done only for the true predation rates of a 4- and a 7-month period because approach 3 does not rely on this assumption.
2. Changing the difference in calf mortality because of unknown factors between the two areas by up to 100% in increments of 10% from an initial value of 12% on an annual basis (Gundersen 2003). Because we adjusted calf mortality rates to the length of observation (i.e., 4, 7, and 11 months), all approaches should have the same bias.
3. Changing the difference in cow mortality because of unknown causes between the two areas by up to 100% in increments of 10% from an initial value of 0.01 on an annual basis (Gundersen 2003). Because we adjusted calf mortality rates to the length of observation (i.e., 4 and 7 months), bias should be equal irrespective of length of observation (approach 3 does not violate this assumption). Results from our simulations are presented as the percentage bias from the true value.

Statistical analysis

CCs (and variance estimates) used in approaches 1 and 2 were calculated using a normal response model with identity link function, treating each independent management unit (approach 1) and aerial survey (approach 2) as sampling units. Survival rates used in approach 3 were calculated as the proportion of calves surviving from June to April. The survival rates (and variance estimates) where achieved using a binomial response model with logit link function. Harvest rates (and variance estimates, approach 2) were also achieved using a binomial response model with logit link function, treating each independent management unit as sampling units. We used the delta method (e.g., Greene 2003) to approximate the variances of predation rates (Eqs. 4, 7, and 8) and kill rates given the variance of the function components (see Greene 2003 for details).
        Statistical tests were based on generalized linear models in the macro GLIMMIX implemented in the SAS software (Littell et al. 1996). When needed, we used repeated measures models to calculate test statistics. To describe the changes in harvest through time and the difference in CCs in approach 1, we used the management unit as subjects in repeated models. In approach 3, we used the individual cow as the subject in repeated analyses comparing calf survival between areas.

Table 1 Monthly predation rate of calves (±SE) based on the three different approaches: (1) hunter observations, (2) aerial surveys, and (3) visual observation of calf survival from radio-collared cows

Approach	1996/1997	1997/1998	1998/1999	1999/2000	2000/2001	2001/2002
1	0.059±0.031	0.032±0.024	0.041±0.026	0.017±0.024	0.013±0.024	*−0.084±0.016*
2				0.134±0.081	0.071±0.029	*−0.051±0.015*
3				0.061±0.004	0.017±0.003	0.004±0.002

The two negative predation rates in italics indicate higher mortality of calves outside than inside the wolf pack territory.

Results

Estimated predation rates
Approach 1—hunter observations

Within the complete study area, 8,183 calves and 14,154 cows were observed and reported by hunters during 64,565 hunter-days (19,711 inside and 44,854 outside) in the period 1994 to 2001. Before the colonization of wolves in 1996/1997, CCs did not differ outside and inside the Koppang territory ($F_{1, 17}=0.010$, P=0.936; Fig.

2b). During the 5 years from 1996 to 2000, there were on average 0.08 (SE=0.04) more calves per cow outside than inside the Koppang territory ($F_{1, 17}$=3.66, P=0.073). The estimated monthly predation rate on calves from June to September for these 5 years (1996/2000) ranged approximately between 1 and 6% (Table 1).

In 2001, however, we observed 0.27 (SE=0.09) more calves per cow inside than outside the Koppang territory ($F_{1, 17}$=10.24, P=0.005) indicating higher mortality of calves outside the wolf pack territory than inside (yielding the negative predation rates in Table 1).

Approach 2—aerial surveys
Based on aerial surveys, the CC in December was higher outside than inside the wolf territory in 1999/2000 and 2000/2001 (both contrasts F>10.75, P<0.021; Fig. 3). From these CCs, we estimated approximately 10% monthly predation rate of calves from June to December as an average for the 2 years (Table 1).
Similar as for approach 1, we found higher CCs inside than outside the wolf pack territory during the winter survey of 2001/2002. Although this difference was not statistically significant ($F_{1, 18}$=0.77, P=0.421), it indicates higher mortality of calves outside the wolf pack territory than inside (see Table 1).
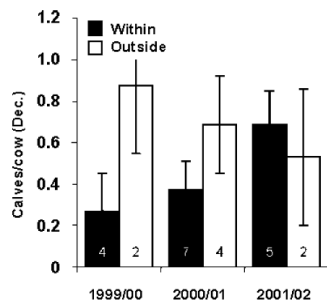
Fig. 3 Calf/cow ratios (±2 SE) from aerial surveys. Numbers innside columns are the number of helicopter surveys

Approach 3—radio tracking
The number of calves monitored inside the wolf territory was 18, 15, and 20, in 1999/2000, 2000/2001, and 2001/2002, respectively, whereas the number monitored outside was 7, 2, and 9, for the same years. Because of the low number of collared cows residing outside the Koppang territory in some years, we pooled data from all 3 years when estimating calf survival outside the Koppang territory. This yielded a mean survival rate of 0.89 (95% confidence interval [CI]=0.63–0.97) for the 11 months of observation. In contrast, the 11-month overall calf survival inside the wolf pack territory was 0.68 (95% CI=0.54–0.79). The survival rates tended to vary among years ($F_{1, 35}$=3.35, P= 0.054) with an estimated mean (95% CI) of 0.45 (0.24– 0.67), 0.73 (0.46–0.90), and 0.85 (0.62–0.95) in 1999/2000, 2000/2001, and 2001/2002, respectively. According to Eq. 8, these survival rates yielded monthly predation rates of calves from June to April up to 6% (mean=0.027 [SE= 0.013]) for the 3 years analyzed (Table 1).
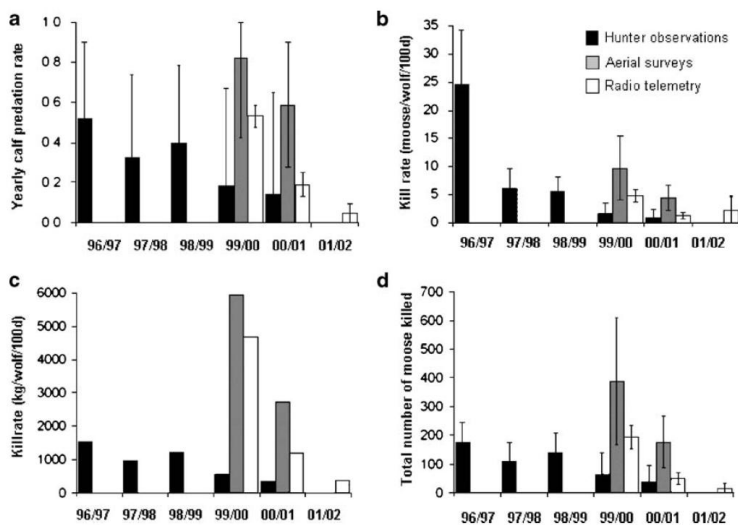
Fig. 4 a Annual calf predation rates, **b** total kill rates estimated as the number of moose/wolf/100 days, **c** total kill rates estimated as the body mass of moose (kg) per wolf per 100 days, and **d** the total number of moose killed based on the difference in calf/cow ratios

from hunter observations, aerial surveys, and survival of calves from radio-collared cows, respectively. To transform from predation rates to kill rates, we used estimates of moose population size and population age and sex structure shown in Fig. 2. Estimates from hunter observations and aerial surveys (approaches 1 and 2) for the last year (2001/2002) were negative and are not presented in the figures (see Table 1)

Annual number of kills
In Fig. 4, we have transformed the monthly predation rates shown above to yearly estimates of predation rates on moose calves (Fig. 4a). We have further estimated total kill rates as the number of moose per wolf per 100 days (Fig. 4b) and as the body mass of moose (kg) per wolf per 100 days (Fig. 4c). Finally, we also estimated the total number of moose killed (Fig. 4d). Considerable variation existed among years and methods, but there was a general trend of decreasing predation rate over time.

Violation of assumptions
When the true predation rate is low (annual predation rate= 0.05), the sensitivity analyses indicated that increasing fecundity by 10% inside (e.g., 0.87 calves per cow, instead of 0.79) underestimated the annual predation rate of calves by 628 and 337% if based on observations in September and December, respectively. The same parameter values under a high predation rate (annual predation=0.4) yielded underestimates of 50 and 27%, respectively. The bias increased exponentially with increasing fecundity inside (Fig. 5a and b). With increasing fecundity outside, the predation rate was overestimated but to a lower degree. The bias approached an asymptote with further increases in fecundity outside (Fig. 5a and b).
Bias was a linear function of the percentage increase in calf mortality from unknown causes inside the wolf territory (Fig. 5c and d). A 10% increase in the annual mortality rate of calves from unknown causes would overestimate calf predation rate by 28.4 and 2.2% when the true predation rate was low and high, respectively (irrespective of time of observation). Bias showed a slight exponential relationship to increasing calf mortality outside relative to inside the wolf territory. A 10% higher mortality rate because of unknown causes in calves outside than inside underestimated the annual predation rate of calves by 28.8 and 2.3%, at low and high true predation rates, respectively.

Bias increased linearly by 0.15 and 1.92% for a 10% increase in cow mortality outside (overestimate) or inside (underestimate) the wolf territory. However, actual mortality of cows from unknown causes is low, and we expect a higher rate of cow mortality inside because of predation. By using the observed ratio of wolf killed cows per wolf killed calf (3 of 19) inside the territory (see "Materials and methods"), we underestimated the annual predation rates of calves between 8.6 and 12.1% (highest bias in September at low predation rates).
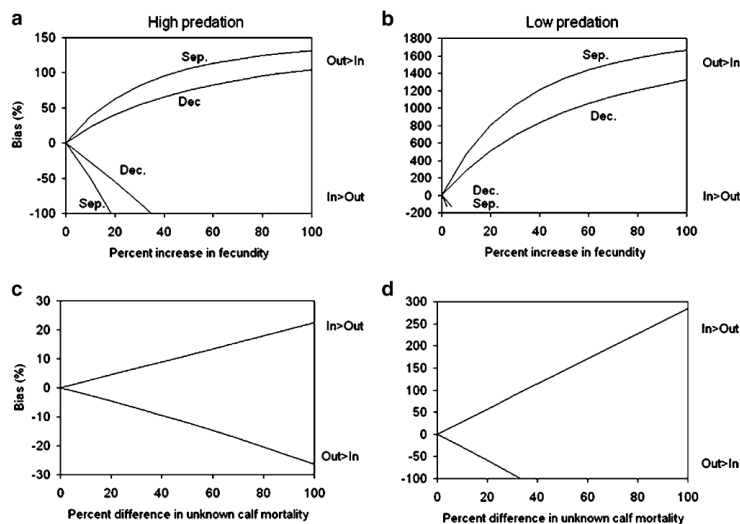
Fig. 5 The sensitivity (percent bias) of violating the assumptions under high (annual predation rate=0.4) and low (annual predation rate=0.05) predation. Bias depending on differential fecundity in the two areas, presented as increased fecundity either outside or inside the wolf territory (a and b). Bias depending on unequal calf mortality outside and inside wolf territory (c and d). Out > In and In > Out present bias when fecundity or calf mortality is higher outside than inside and inside than outside, respectively

Discussion

Our results indicated that estimated predation rates varied considerably among years, as well as among methods used. In general, predation rates decreased during the course of the study for all methods employed. Despite similar trends, the three methods produced different predation rate estimates and subsequently different kill rate estimates. Aerial surveys produced the highest estimates, whereas hunter observations produced slightly lower

estimates than those based on telemetry. This suggests that one or several assumptions has been violated, that some methods were more accurate than others, or that the methods are not directly comparable (e.g., because of different times of year used in the different methods).

Given the large number of assumptions, there may be several reasons for the differences observed between methods. One possibility is that predation pressure varies through the year (e.g., Smith et al. 2004). If predation rates are higher during winter than during summer, we would expect that predation rates estimated by approaches 2 and 3 (summer and winter) to be higher than those estimated by approach 1 (only summer). However, recent Scandinavian studies found higher predation rates during summer than winter (Wabakken et al. 2004), which contradicts the low predation rates estimated by approach 1. Irrespective of direction, however, large variation in predation rate during the year will complicate estimating annual predation rates based on short study periods. Until more is known about seasonal variation in predation rates in Scandinavia, methods involving longer predation periods (e.g., method 3) should be preferred.

Violating the assumption of equal calf and cow rates of mortality because of causes other than wolf predation within and outside the wolf territory is another potentially important source of bias. We believe this is a fair assumption during the summer but not necessarily when hunting mortality and early winter mortality are included. In this case, there is an increasing probability of unequal mortality rates between areas, which could lead to biased predation rates. If cow mortality is low, bias because of different cow mortality rates makes only minor changes to estimated predation rates. Predation on cows is expected to underestimate predation rates in approach 1 and 2 by up to about 12% because it deflates the CC inside the wolf area. Unequal mortality in the two areas would be most problematic at low levels of predation and when the CC has been estimated early in the season (i.e., relatively higher bias in approach 1 than in approach 2). However, because more mortality factors are introduced with time since parturition (e.g., vehicle accidents during winter; Gundersen 2003), method 2 is more likely to produce biased estimates than method 1. Method 2 produced some very high predation rates. If this was due to unequal calf and cow rates of mortality as a result of causes other than wolf predation within and outside the wolf territory, this was most likely due to higher mortality of calves inside than outside. This is because we expect higher mortality of cows inside than outside because of predation, which would have caused us to underestimate predation rates. In contrast, the method using hunter observations produced only slightly lower estimates than method 3. This supports previous findings that the CCs observed by hunters are good estimates (Solberg and Sæther 1999; Ericsson and Wallin 1999) and that no serious violations of assumptions occur during the short period from the calving season to September.

Favorable conditions for using hunter observations may not prevail in all years or in other areas. For example, in Koppang, the observed CCs in the last year of study were higher within than outside the wolf territory, indicating that factors other than predation affected the ratios. Possibly, this was due to a low sample of observations after less intensive hunting 2 years in a row. More likely, however, it reflects a change of hunting practice inside the wolf territory. Because of the impact of wolf predation on moose calves, hunters within the wolf territory reduced their hunting effort on calves during the last 2 years. This probably affected the CC observed during the entire hunting season (i.e., hunters inside observed more calves per cow). This explanation was also supported by the higher CC observed within relative to outside the territory during the aerial surveys in the last year. Moreover, the reduction in wolf numbers, from 11 to 2 in the pack, may partly explain the low predation rate estimated the last year. Because it was not known when the new male arrived, the resident female may have been alone in the Koppang territory during the first half of that year.

The high kill rate observed in the first year may be explained by the fact that the pack consisted of only two members during the first year. A number of studies have documented that individual kill rate tends to increase with decreasing pack size (e.g., Thurber and Peterson 1993; Hayes et al. 2000), partly because of less efficient use of the kill (Thurber and Peterson 1993). The contrasting kill rates between the first and the last year of study when there were two wolves present may then be explained by the lack of an alpha male the last year giving less efficient hunting for large animals as moose. At the same time, the moose in the area were completely inexperienced with wolves after wolf colonization the first year, which may have made them particularly vulnerable to predation (Berger 1999). High vulnerability of inexperienced moose to predation from recolonizing bears has previously been documented in Sweden (Berger et al. 2001), and inexperience with wolves may similarly increase moose vulnerability to predation.

Method 3 invoked the least number of critical assumptions for estimating predation rates. The predation rate of calves was estimated directly by comparing the proportional loss of calves from radio-collared cows inside and outside the wolf territory. Thus, besides sampling errors, the only fundamental assumption is that mortality other than predation and harvesting (which is accounted for) was similar outside and inside the territory. We believe this is a reasonable assumption, and a similar method should therefore be used for estimating predation rates in other age and sex groups. As an alternative, we estimated predation rates of the adult sex and age groups by their proportional occurrence in the recorded winter kill of wolves in the area. We assumed that the sex- and agespecific distribution of moose killed by wolves did not differ among seasons.

We conclude that direct observations of kills, for instance by radio telemetry, is by all means the best

alternative to approach unbiased estimates of absolute kill rates. Monitoring radio-collared moose also gives an opportunity to quantify other sources of mortality, including the effect of other predators (Ballard et al. 1981) and expand the gain of information as shown by Swenson et al. (2001) who documented a compensatory increase in fecundity of moose cows that lost their calf/calves to bear predation in Sweden. However, all three methods seem to give relative values, which might be appropriate to question trends trough time or between areas. Hence, in spite of its crude estimates of predation rates, hunter observations may be useful to question large-scale trends in space and time. Hunter observations are registered annually by all hunting teams in Norway and give an efficient way of addressing large-scale variations in predation pressure. This compared to methods such as radio telemetry or aerial survey, which may have logistic (e.g., economic or labour intensive) limitations in time and space.

Acknowledgments

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