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Original article

Spatio-temporal relationship between calf body mass and population productivity in Fennoscandian moose *Alces alces*

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Body mass is an important life history trait related to survival, mating success and fecundity in ungulates. Accordingly, we may expect that both body mass and reproductive measurements at the population level can be used as valid indices of population condition. However, several factors may modify the relationship between body mass and fecundity because of trade-offs between maturity and early body growth, and varying mortality patterns and sex/age structure among populations. To evaluate the use of such indices for population monitoring and examine the current variation in moose *Alces alces* population condition in Fennoscandia, we studied the spatio-temporal relationship between calving rate, twinning rate and average autumn calf body mass of moose in Norway and Finland. Calving rate and twinning rate were based on moose observations by hunters while body mass was the average carcass mass of harvested calves. We found a positive relationship between indices both within and among populations. Calves were on average heavier and the observed recruitment rates higher in Finland than in Norway, which is consistent with the higher moose density and presumably lower primary productivity (higher altitude) of moose ranges in Norway. We also found higher observed recruitment rates in populations and years with more even adult sex ratios (females per male) and low relative harvest rates of calves. This suggests that variation in recruitment rate is not only a matter of nutritional condition, but is also affected by varying hunting regulations and harvest structure. For monitoring purposes, we believe that twinning rate is best suited for ranking populations according to nutritional status as this index is closely related to fitness and is relatively insensitive to variation in perinatal and harvest mortality. However, variation in calf body mass may better reflect temporal variation in living conditions. This is because early body growth is sensitive to variation in food availability (and quality) and because body mass may respond more instantaneously than recruitment indices to adverse conditions. Accordingly, we found both calving rate and twinning rate to be best related to variation in mean calf body mass in the previous year.

Key words:Alces alces, body mass, Fennoscandia, moose, population monitoring, population productivity, recruitment rate

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Body mass is an important life history trait in ungulates as large body masses are related to high survival, mating success and fecundity (Stearns 1992, Bérubé et al. 1999, Gaillard et al. 1996, 2000b). In many species, larger females also produce larger than average offspring (Gaillard et al. 1992, Sæther & Haagenrud 1985, Sand 1996, but see Gaillard et al. 2000a), which correspondingly tend to become larger adults (Albon et al. 1987, Festa-Bianchet et al. 2000, Beckerman et al. 2002, Solberg et al. 2004, 2007). The positive relationship between early growth, and adult size and fecundity suggests that body mass variation of young individuals should influence the population dynamics (e.g. Gaillard et al. 2000b, Hewison & Gaillard 2001), and hence a positive relationship between the average size of juveniles and population productivity could be expected (Kie et al. 2003, Stewart et al. 2005).

This assumed positive relationship between life history traits is often utilised for monitoring exploited ungulates (Hanks 1981, Solberg et al. 1999, Herfindal et al. 2006, Boertje et al. 2007). For instance, by measuring the variation in average body mass (or condition) of harvested juveniles, wildlife managers can keep track of the population vigour and nutritional status (e.g. Morellet et al. 2011). However, like the relationship between life history traits within individuals, several factors may modify the relationship between body mass and fecundity at the population level. First, a trade-off between maturity and body growth may be shaped by different mortality (harvest) patterns among populations (Proaktor et al. 2007). Accordingly, females may mature at different ages and sizes among populations, leading to varying relationships between juvenile size, age at first reproduction and adult fecundity at the population level (Stearns 1992, Garel et al. 2009, Monteith et al. 2009). Second, high productivity can be associated with low offspring size in species that produce multiple young (Stearns 1992, Nygrén 2003) suggesting that populations with high productivity are not necessarily associated with larger offspring. The fact that ungulates are long-lived animals may also complicate the matter. Following improved living conditions, fecundity and offspring size may reflect past rather than current conditions, which in turn can have different effects on the size and number of offspring. Indeed, although small females tend to produce smaller offspring, they may still produce large litters when the environmental conditions are good (e.g. Monteith et al. 2009).

In Fennoscandia, the abundance of moose *Alces alces* has been growing during the last 50 years, leading moose to become the most important wildlife resource (Lavsund et al. 2003). Following this increase, there has been growing concern about the potential impact of density-dependent food limitation, and for the same reasons, populations are now regularly monitored for variation in population density and structure and nutritional status. Utilising data provided by hunters (i.e. harvest and observation data) has been the favoured approach for this monitoring. These data include carcass masses of harvested moose and the sex and age of moose observed during hunting from which indices of body growth, reproductive performance, density and adult sex ratio are derived (e.g. Lavsund et al. 2003, Morellet et al. 2011).

The most common indicators of population nutritional status are the mean carcass mass of harvested calves, as well as the calving rate (proportion of females with calf/calves) and twinning rate (females with twins/females with $\geq$ 1 calf) of observed females. To indicate population nutritional status, body mass of calves are usually preferred to the mass of moose in older age groups. This is because calves constitute the most numerous age group in the harvest (our study), can be easily aged by their size and tooth pattern (Rolandsen et al. 2008), and because the sample of harvested calves is not assumed to be affected by hunting selectivity (e.g. Moe et al. 2009). By being the youngest, smallest and arguably the weakest individuals in the population, we may also expect them to quickly respond to annual variation in living conditions (Gaillard et al. 2000b, Herfindal et al. 2006).

Large numbers of moose observations are inexpensive to collect and data can be easily converted to indices of population nutritional status, such as calving rate and twinning rate (i.e. recruitment rates). However, because these data are collected in autumn (i.e. about 4-6 months after calving) and while hunting, their ability to reflect the variation in population condition with adequate precision has been questioned. Large variation in predation pressure can for instance lead to large variation in recruitment rates among regions and over time; variations that are mostly unrelated to population nutritional status (Boertje et al. 2007). In addition, annual variation in female age structure and adult sex ratio (Solberg et al. 2002, Sæther et al. 2004, Nygrén 2009) can affect population productivity. These effects are particularly relevant for harvested species because biased harvesting of sex and age groups can create large variation in population structure (e.g. Ginsberg & Milner-Gulland 1994, Solberg et al. 1999, Mysterud et al. 2005, Nygrén 2009).

In our study, we analysed the spatio-temporal variation in moose body mass and recruitment rates at the population level, and evaluated the usefulness of these data for monitoring purposes. We did this by first testing the extent to which body masses of calves and calving/twinning rates (recruitment indices) varied among regions and countries. In general, we expected the calf body mass and recruitment indices to be higher in Finland than in Norway, given the current higher densities of moose in Norway (see below), and males to be heavier than females. Next, we tested if the recruitment indices were related to the variation in calf body mass within (temporal relationship) and among regions (spatial relationship), while simultaneously controlling for varying hunting selection and population sex ratios. To better understand the functional relationship between body mass and recruitment rates, we tested the temporal relationship at several time lags. If both calf mass and fecundity depend on resources available in the year of reproduction (as in income breeders; Jönsson 1997), we expected the recruitment rates to be positively correlated with the mean calf body mass in the same year. However, as calf body mass can have long-lasting effects on adult size and fecundity (Keech et al. 1999, Solberg et al. 2004), the temporal variation in recruitment rate may also be a time-delayed response to a change in calf body mass. The latter relationship is generally assumed among moose managers, and could favour monitoring juvenile body mass as a means to foresee changes in population productivity. However, convincing support for such a relationship has yet to be presented.

Material and methods

Study areas in Finland and Norway

Our study area covers populations from most of the distributional range of moose in Norway and all of Finland (Fig. 1). In Norway, our study areas are part of the national monitoring programme for cervids (Solberg et al. 2006), whereas in Finland, our study areas constitute the 15 game management districts (Nygrén & Pesonen 1993). The data for body mass of calves and moose observations were aggregated from subregion-level (municipality in Norway and game management association (mostly based on municipalities) in Finland) to these region-level mean values.

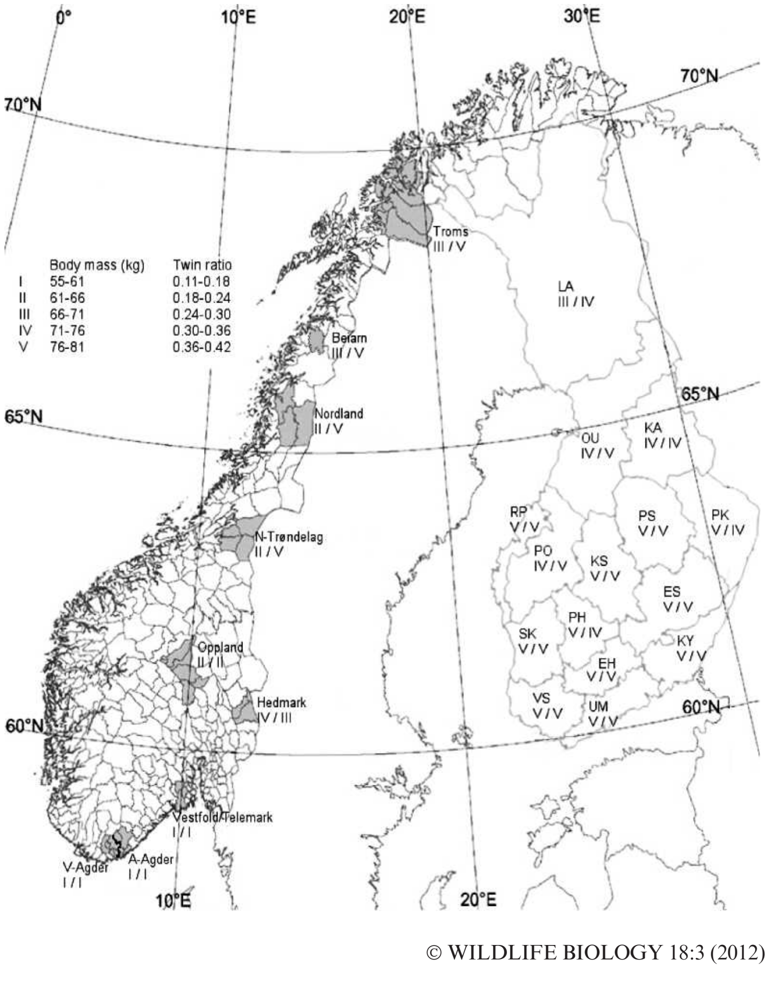

Figure 1. Our study areas in Norway (Vest-Agder, Aust-Agder, Vestfold/Telemark, Hedmark, Oppland, Nord-Trøndelag, Nordland, Beiarn and Troms) and Finland (EH = Etelä-Häme, ES = Etelä-Savo, KA = Kainuu, KS = Keski-Suomi, KY = Kymi, LA = Lappi, PH = Pohjois-Häme, PK = Pohjois-Karjala, PO = Pohjanmaa, PS = Pohjois-Savo, RP = Ruotsinkielinen Pohjanmaa, SK = Satakunta, VS = Varsinais-Suomi and UM = Uusimaa). The numerals I-V indicate the category of mean body mass of female calves and the twinning rate in the region, category I being the lowest and V the highest values, respectively.

Finland and Norway are found at the same latitudes (see Fig. 1), and are covered mainly by the same vegetation types. Both countries are dominated by coniferous forests. However, Norway has a more oceanic climate than Finland, and due to the more mountainous topography, moose areas are generally found at higher altitudes. For more details on our study areas in Norway, see Solberg et al. (2002) and Garel et al. (2009), and in Finland, see Nygrén et al. (2007).

Moose population density, management and monitoring in Finland and Norway

In both Norway and Finland, moose populations began to increase in the 1960s and reached a peak in Norway in the 1990s. In Finland, the moose population has peaked twice: first in the late 1970s and early 1980s and again in the late 1990s and early 2000s (Lavsund et al. 2003, Nygrén 2009). Currently, the density of moose in Norway is almost twice the density in Finland (approximately 0.8-1.1 moose/km^2 in Norway and 0.2-0.5 moose/km^2 in Finland), mainly because of the official enforcement of relatively moderate density thresholds in Finland (Nygrén 1984, Nygrén & Pesonen 1993, Lavsund et al. 2003, Nygrén 2009). Otherwise, the principles of moose management are quite similar in these countries (Lavsund et al. 2003). Moose hunting occurs in autumn at much the same period (September-December), but the hunting season has varied somewhat over time and is much shorter in Norway (Nygrén et al. 2007, Garel et al. 2009). Hunting is mainly carried out by a group of hunters in a team, often with the use of dogs and/or beaters to flush out moose from cover (Koskela & Nygrén 2002, Ruusila & Pesonen 2004).

Moose harvesting is based on a quota system and the number of harvested moose is obligatorily recorded and reported according to sex and age (calf, yearling and adult ($\geq$ 2 years old) in Norway, calf and adult ($\geq$ 1 year old) in Finland), and moose observations (see below) are collected by hunters as a standard routine during the hunt (Lavsund et al. 2003). In both countries, body mass (carcass mass) of harvested moose has been systematically collected in many areas over several years (Solberg et al. 2006, Nygrén et al. 2007; see Fig. 1). We only used data from 1991-2006 in our study so that our study period was the same in both countries.

Observation data

Moose observation monitoring in Norway and Finland is a systematic recording of the sex and age (calf or adult) of moose observed by moose hunters during the hunting season (Lavsund et al. 2003). In both countries, hunting effort is measured as the number of hunting days, either by the hunting team (Finland) or by the individual hunters (Norway). The observations are classified according to six categories: calves (in Finland calculated from observed females with one calf or twins), adult ($\geq$ 1 year old) males, adult females without calf, females with one calf, females with twins and individuals of unknown sex and/or age (Nygrén 1984, Nygrén & Pesonen 1993, Solberg et al. 2006). In Finland, observations are recorded on a daily basis, whereas in Norway only the sum of daily values for the entire hunting season is reported. Because the hunting season is longer in Finland (9-12 weeks) than in Norway (four weeks), we used moose observations only from the first four weeks of hunting in Finland. Currently, more than 5,000 hunting clubs with about 100,000 hunters report 200,000-400,000 moose observations in Finland. The similar figures in Norway are about 60,000 hunters reporting approximately 200,000-250,000 observations each year (Rolandsen et al. 2004, Solberg et al. 2006).

Several indices of population structure are calculated from the observation data (e.g. Nygrén & Nygrén 1976, Nygrén & Pesonen 1993, Solberg & Heim 2002, 2006, Lavsund et al. 2003, Nygrén 2009). The most important are indices of population/regional productivity; 'calves/100 adults' (seen calves per adult in Norway), 'calves/100 females' (seen calves per female in Norway), 'seen proportion of females with calves' and 'seen proportion of females with twins of all females with calf/calves', as well as an index of population sex ratio; 'seen females per male'. In addition, population density is indexed by the number of observations per unit hunting effort (i.e. in Norway, as moose seen per hunter day, and in Finland, as moose seen per team-hunting day). In Finland, population density is also indexed by the numbers of moose that the hunters estimate to be living on their hunting grounds after the hunting season. Despite the rather crude sampling procedure and several possible confounding variables (e.g. variation in weather, hunting skills, number of hunters and hunting methods), the observation data are found to provide good information on the temporal changes in recruitment rate, population density and adult sex ratio among populations (Ericsson & Wallin 1994, 1999, Sylvén 1995, Solberg & Sæther 1999, Solberg et al. 2002, Mysterud et al.

2007, Rönnegård et al. 2008, Bjørneraas et al. 2009), provided that the number of observations is relatively high (Ericsson & Wallin 1994, Sylvén 2000).

Body mass

As a measure of variation in calf body mass, we used the carcass mass of harvested calves during 1991-2006. The carcass mass of calves constitutes about 50% of their live body mass (Wallin et al. 1996). Because carcass mass of calves tends to increase during the hunting period (e.g. Solberg et al. 2004), we adjusted all masses to 15 October by using a regression of carcass mass on kill date within country. In total, we had body mass data from 16,841 calves (8,742 males and 8,099 females) in Norway and from 152,034 calves (80,059 males and 71,975 females) in Finland. The number of calves among the combinations of year and region (N=384) ranged between 10 and 1,834, ensuring that the mean carcass mass constituted a relatively precise reflection of the mean calf body mass in the region (in Finland, game management district, and in Norway, the monitoring area; see Fig. 1). In the forthcoming text, carcass mass is referred to as body mass.

Calf production

Calf recruitment was measured as calving rate and twinning rate. Calving rate is the seen proportion of females with calf/calves during the hunting season, whereas twinning rate is the seen proportion of females with twins of all females with calf/calves. Because moose are harvested while observations are recorded, it is likely that variation in harvest pressure and structure may affect the estimated recruitment rates (Grøtan 2003). For instance, in regions with a high harvest of calves per harvested female, both recruitment rate indices are likely to decrease during the hunting season (e.g. Grøtan 2003, Moe et al. 2009). Such effects are regularly controlled for in Finland, where harvest and observation data are recorded on a daily basis, i.e. the pre-harvest recruitment rates can be estimated (Nygrén & Pesonen 1993, Nygrén 2009). Based on the Finnish data, the effect of variation in the harvesting of calves was found to have only minor effects on the variation in twinning rate, but may have substantial effects on the variation in calving rate. Particularly pronounced effects on the calving rate are expected in regions where the number of harvested calves per harvested female deviates much from the observed calves per female, and *vice versa* (Grøtan 2003).

Since the Norwegian observation data were aggregated over the entire hunting season, we were not able to adjust these observations for variation in the harvest of calves per female. We used unadjusted indices from both countries and statistically controlled varying calf harvesting by including a calf harvest index as a covariate in the analyses. The calf harvest index was calculated as the number of calves per female in the harvest divided by the number of calves per female in the observations. High values indicate that hunters shoot more calves per females than the ratio found in the region. Accordingly, the observed proportion of calves (calving/twinning rate) can be expected to be lower than in the pre-harvested population.

Statistical analyses

We first examined the variation in mean body mass of calves, as well as the calving rate and twinning rate within and among regions (for all variables, N=384) in Finland and Norway using linear models. We expected lower body masses and recruitment rates in Norway than in Finland, and higher mean body mass of males than females. Likewise, we examined the relationship between calving rate and twinning rate within regions expecting a general positive relationship between recruitment indices over time, given the fact that both ratios are likely to be affected by female body condition (Sand 1996).

We then tested to what extent the variation in annual calving or twinning rate was related to variation in mean calf body mass. In these analyses, we used only the body mass of female calves as the body mass of females directly affects the body mass of the offspring (e.g. Keech et al. 2000). Because the calving rate and twinning rate are proportions, both variables were first arcsine transformed (arcsine ($\sqrt{p}$), where p is the ratio; Sokal & Rohlf 1995) to approximate a normal distribution.

To facilitate the interpretation of the spatio-temporal effects of calf body mass, we added both the annual mean body mass and the regional mean body mass in the models. These variables were calculated by first centring the annual mean body mass ($Y_{t,r}$) relative to the mean body mass across all regions and years (μ_y):

$$Y^{s}_{t,r} = Y_{t,r} - \mu_y,$$

where t is year (1991-2006) and r is region. We then calculated the regional mean body mass (μ_r) as:

$$\mu_r = \frac{1}{n_r} \sum Y^{s}_{t,r},$$

where n_r is number of years within region and the sum is over all years and the centred annual body mass ($Y^{ss}_{t.r}$) as:

$$Y^{ss}_{t.r} = Y^{s}_{t.r} - \mu_r.$$

By splitting body mass into regional mean (μ_r) and centred annual values ($Y^{ss}_{t.r}$), we could specifically test to what extent the relationship between recruitment rates and body mass was due to among-region variation (spatial variation) or within-region variation (temporal variation), respectively (Singer 1998). The centred and mean body mass values were not correlated $r < 0.01$). Using centred values, the main effects are also biologically interpretable even when involved in interactions (Schielzeth 2010).

We analysed the variation in recruitment rates using linear mixed effect models with annual recruitment rate (twinning or calving rate) as a dependent variable and with regional mean (μ_r) and annual centred body mass ($Y^{ss}_{t.r}$) of female calves as covariates. For the temporal effect, we tested the variation in recruitment rate (calving and twinning rate) against the variation in body mass in the current year (year t) as well as in the three previous years (year t-1, t-2 and t-3). We also included the observed sex ratio (females per male) and calf harvest index as covariates. We did not include country in these analyses as there was only a small overlap in annual mean body mass between countries. We expected lower recruitment rates in years and regions with a female-biased sex ratio and a high calf harvest index (more calves removed during hunting and hence decreasing calf observations during the harvest season), all else being equal.

To provide a baseline model against which we could compare the more complex models, we estimated the variance components in a model with only region included as a random factor. Two variance components were extracted from this model, representing the variances in twinning or calving rate that are attributed to variation within (residual variance) and among regions. Based on this model, we could 1) determine to what extent the annual twinning or calving rate varied among regions, and 2) estimate the fraction of explainable variation accounted for by the fixed effects in the more complex models. Following Singer (1998), we computed the proportion of explainable variation as:

$$(VC1-VC2)/VC1,$$

where VC1 and VC2 are the variance components in the baseline and the more complex model, respectively (see also e.g. Solberg et al. 2007 for the use of this method).

We considered the models with the lowest Akaike information criterion (AIC) score to be the most parsimonious and thus the 'best' model applied to the data (Burnham & Anderson 2002). We used AIC_c (corrected AIC) to account for the relatively high number of covariates compared to the number of years and regions. We started the model selection with addressing the overall model first and then all the possible nested models of the overall model. Altogether, 13 different models were tested, both for twinning rate and calving rate, from which models that differed in AIC_c by two or less ($\Delta AIC_c \leq 2$) were considered to be equally well supported by the data (Burnham & Anderson 2002). We also computed the Akaike weights to compare the relative performance of models, where the strength of evidence in favour of one model over another is the ratio in AIC weights between the two models (Burnham & Anderson 2002). Since we were comparing models with different fixed effect structure, we used Maximum-Likelihood (ML) for model selection (Singer 1998, Crawley 2002) and Restricted Maximum-Likelihood (REML) for parameter estimation. All the statistical analyses were performed using SPSS 19.0 for Windows.

Results

Variation on calf body mass

On average, calves were heavier in Finland than in Norway (see Figs. 1 and 2). The body mass (see Fig. 2) of male calves ranged from 25 to 120 kg in Finland (mean = 81 kg, SD = 7, N = 4,264) and from 44 to 96 kg in Norway (mean = 67 kg, SD = 7, N = 489). The corresponding figures for female calves (see Fig. 2) were 40-107 kg (mean = 77 kg, SD = 7, N = 4,245) and 28-91 kg (mean = 63 kg, SD = 7, N = 488), respectively. The variation among populations is shown in Fig. 1.

There was a strong positive relationship between annual mean body mass of male and female calves in both countries during our study period, 1991-2006 (Finland: $r = 0.618$, $SE = 0.013$, $t = 48.348$, $P < 0.001$; Norway: $r = 0.677$, $SE = 0.039$, $t = 17.514$, $P < 0.001$). Male calves were approximately 5% heavier than female calves (in Finland, the mean difference was 4.2 kg, and in Norway, it was 3.5 kg). In both countries, there was an overall negative trend in body mass (see

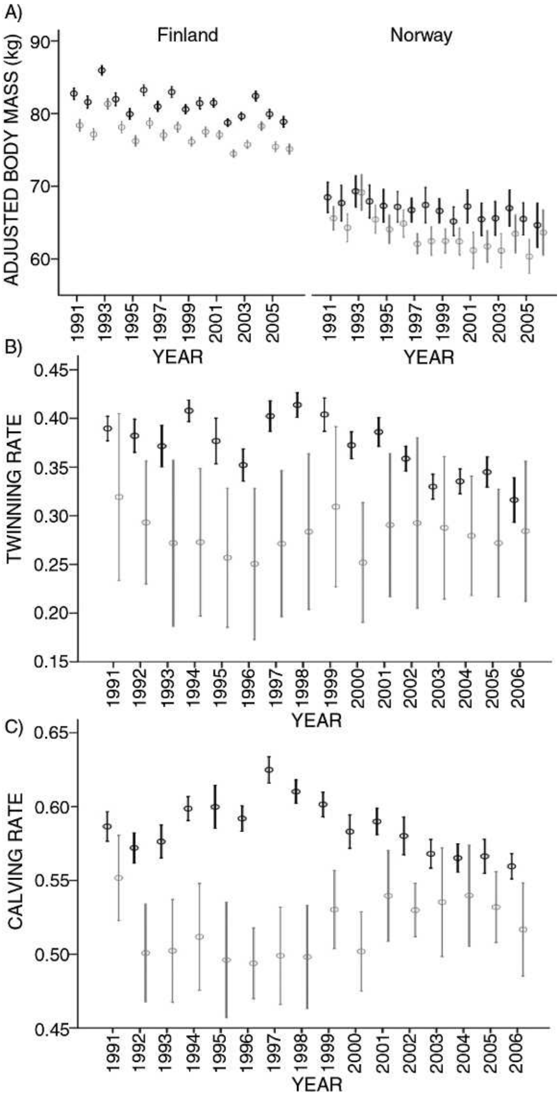

Figure 2. Annual variation in A) mean body mass of calves (males black, females grey), B) twinning rate and C) calving rate in moose populations in Finland (black) and Norway (grey) during 1991-2006. Calf body mass is carcass mass adjusted for variation in kill date.

Fig. 2; Finland: r = -0.223, SE = 0.017, t = -13.088, P < 0.001; Norway: r = -0.277, SE = 0.053, t = -5.243, P < 0.001) during our study period.

Variation in calving rate and twinning rate

Calf recruitment was generally higher in Finland than in Norway (see Figs. 1 and 2). On average, 59% of all adult females were seen with a calf/calves (i.e. calving rate) in Finland (mean = 0.59, SD = 0.07, N = 8,504) and 51% in Norway (mean = 0.51, SD = 0.82, N = 936). Similarly, 38% of the calf-rearing females in Finland recruited twin calves (i.e. twinning rate, mean = 0.38, SD = 0.09, N = 8,504) compared to only 28% in Norway (mean = 0.28, SD = 0.14, N = 936). The spatial distribution in population productivity can be seen in Fig. 1. Generally, there was a positive relationship between the annual twinning rate and calving rate within populations in both countries but with large variation among years (Finland: r = 0.821, N = 16; range among years: -0.031-0.622, N = 15, P = 0.013-0.978; Norway: r = 0.725, N = 16; range among years: -0.003-0.937, N = 15, P = 0.001-0.994).

Spatio-temporal covariation between calf recruitment and female calf body mass

The best linear mixed effect models explaining the variation in twinning rate and calving rate included regional mean body mass (μ_r), centred annual mean body mass ($Y_{t,r}^{ss}$) and the observed adult sex ratio. In addition, region was included as a random factor (Table 1). Also the calf harvest index was included in some of the best models, but were much less supported (the best models twinning rate and calving rate were 2.9 and 1.4 times more supported than the second best models, respectively). On average, calf recruitment was higher in regions and years with high mean body mass. We also found the effect of centred annual mean body mass ($Y_{t,r}^{ss}$) to be stronger in regions with high mean body mass (positive regional mean body mass (μ_r)*centred annual mean body mass interaction ($Y_{t,r}^{ss}$)). However, this effect was significant for twinning rate but not for calving rate (Table 2), probably because the high calf harvest affects the ratio of calves per females observed during harvest season. The strongest effect of centred annual mean body mass was found with a time lag of one year (year t-1), indicating that the growth conditions during the previous summer were most important for the variation in recruitment rate (see Table 2).

The negative effect of adult sex ratio (females per male) was in accordance with expectations, and indicates that higher recruitment rates occur in years and populations with a higher proportion of males. Similarly, we found that higher recruitment rates were recorded in years and regions with a low off-take of calves relative to the calves per female in the region (i.e. low calf harvest index; see Tables 1 and 2).

From a total of 13 models (both for twinning and calving rate), we found four alternative models for twinning rate and calving rate within $\Delta AIC \leq 6$ (see Table 1). Alternative models included or excluded the calf harvest index and regional body mass (μ_r) in year t-1 as a random slope (see Table 1). Hence, the

Table 1. The best candidate models explaining the spatio-temporal variation in twinning rate and calving rate (both arcsine transformed) in Fennoscandian moose using linear mixed effect models and with region as random factor (intercept). X indicates variables included in the model. BM is the baseline model with only region included as random factor (intercept). Models where centred annual mean body mass in year t-1 was included as random slope are marked with an underlined X. ΔAIC_c refers to the difference in AIC_c values between the best model and the candidate model. All candidate models with $\Delta AIC_c \leq 6$ are presented in the table. The best twinning rate model (model 1) explained 26% of the within-region (i.e. temporal) and 49% of the among-region variance compared to the baseline model (BM). The corresponding numbers for calving rate were 38% and 63% (model 1), respectively. Regional mean body mass (μ_r) = rbm and centred annual mean body mass ($Y^{ss}_{t,r}$) in year t-1 = cbmt-1.

Model	Region	Rbm	Cbmt-1	rbm*cbmt-1	Calf harvest index	Adult sex ratio	Within region variance	Among region variance	ΔAIC_c	Akaike weight
Twinning rate										
BM	x						0.001880	0.010940	98.05	0.000
1	x	x	x	x		x	0.001388	0.005632	0.00	0.638
2	x	x	x	x	x	x	0.001388	0.005632	2.10	0.223
3	x	x	$\underline{x}$	x		x	0.001368	0.005632	3.65	0.103
4	x	x	$\underline{x}$	x	x	x	0.001368	0.005632	5.76	0.036
Calving rate										
BM	x						0.001320	0.001440	156.66	0.000
1	x	x	x	x		x	0.000821	0.00528	0.00	0.508
2	x	x	x	x	x	x	0.000821	0.00499	0.67	0.364
3	x	x	$\underline{x}$	x		x	0.000820	0.00521	3.76	0.077
4	x	x	$\underline{x}$	x	x	x	0.000819	0.00495	4.62	0.050

general relationship between recruitment rates and mean calf body mass seemed relatively consistent among the models.

The two best models for twinning rate accounted for about 26% of the variation within regions and about 49% of the variation among regions (see Table 1). The best model for calving rate accounted for about 38% and 63% of the within- and among-region variation, respectively. Adding the calf harvest index increased the explanatory power of the model to 65% of the among-region variance while the within-region variance remained the same 38% (see Table 1). Hence, a larger proportion of the explainable variation in recruitment rates was accounted for among than within regions.

Discussion

Our results show that there is large variation in calf body mass and recruitment rates within (i.e. temporal variation) and among regions (see Figs. 1 and 2), and that the population condition, measured as recruitment rate and the mean body mass of calves, is generally higher in Finland than in Norway (see Figs. 1 and 2). Populations with larger calves are also more productive, as was expected based on the positive body size and fecundity relationship found in moose (Sand 1996, Garel et al. 2009). The annual variation in recruitment rates was best explained by a time-delayed effect of calf body mass, indicating that moose recruitment rates in Fennoscandia

Table 2. Parameter estimates and test statistics for the best models in Table 1 (i.e. models with the lowest AIC_c).

Parameter	Estimate	SE	T	P
Twinning rate				
Intercept	0.672	0.188	35.777	< 0.001
Regional mean body mass (μ_r, rbm)	0.010	0.002	4.732	< 0.001
Centred annual mean body mass ($Y^{ss}_{t,r}$) in year t-1 (cbmt-1)	0.006	0.001	7.291	< 0.001
Adult sex ratio	-0.027	0.005	-5.735	< 0.001
rbm (μ_r)*cbmt-1	0.001	0.000	4.760	< 0.001
Calving rate				
Intercept	0.937	0.009	104.269	< 0.001
Regional mean body mass (μ_r, rbm)	0.003	0.001	4.954	< 0.001
Centred annual mean body mass ($Y^{ss}_{t,r}$) in year t-1 (cbmt-1)	0.003	0.001	4.490	< 0.001
Adult sex ratio	-0.042	0.003	-12.236	< 0.001
rbm (μ_r)*cbmt-1	-0.000	0.000	-0.950	0.343

depends more on accumulated reserves than on resources available in the year of reproduction. We also found higher observed recruitment rates in regions and years with more even adult sex ratio and low relative harvest rates of calves. This suggests that variation in recruitment rate is not only a matter of nutritional status, but may as well be a product of varying hunting regulations and harvest structure.

The positive relationships between recruitment indices and calf body mass in moose support the notion that body condition and reproduction will be lower in populations close to carrying capacity (Kie et al. 2003, Stewart et al. 2005). In Finland, moose densities are generally lower than in Norway (Lavsund et al. 2003) and the moose ranges are found at lower altitudes. Hence, it can be assumed that the primary production on moose land is also higher in Finland than in Norway (Zheng et al. 2004). Following particularly high densities ($>$ 2 moose/km^2), many populations in southern Norway have experienced significant decline in calf body mass and recruitment rates during the last two decades, most likely due to density-dependent food limitation (Lavsund et al. 2003, Solberg et al. 2006). Further north, densities are lower and the feeding conditions better, with the result that the recruitment rates and mean calf body mass increases from south to north (Solberg et al. 2006; see Fig. 1). In Finland, the moose densities are kept relatively low by a strict harvesting regime (Lavsund et al. 2003, Nygrén 2009), providing good condition for body growth and reproduction. Probably for the same reasons, we also see much less variation in body mass and recruitment rates between Finnish than Norwegian populations. However, although the differences in life history suggest that moose densities in Finland are low compared to the carrying capacity, the effects of varying density and habitat productivity on moose population performance in Fennoscandia are still in need of closer studies.

The positive relationship between calf body mass and recruitment indices are also in accordance with previous findings showing that larger moose calves tend to become larger adults (Solberg et al. 2008), which mature at a younger age (Sæther & Haagenrud 1985, Sand 1996), start twin production earlier (Sand 1996, Solberg et al. 2008) and produce larger calves on average (Solberg et al. 2007). Large size is often correlated with high phenotypic quality (Gaillard et al. 2000a, Hewison & Gaillard 2001), and large mothers therefore can allocate more resources to offspring than smaller mothers can (e.g. Loison & Strand 2005). However, because maternal resources can be distributed on varying number of young (Stearns 1992), there is not necessarily always a positive relationship between the size of the mother and her offspring.

In moose, larger females do not seem to trade off calf size for calf number; at least not in populations living under good nutritional condition (Solberg et al. 2007). However, such trade-offs can potentially be more expressed in populations living under food limitation, as may be the case for some regions in Norway. In the populations in Oppland and Nord-Trøndelag, for instance, there are large differences in twinning rate despite hardly any differences in mean calf body mass (see Fig. 1). Possibly, this is because fewer resources available per female in Oppland (low twinning rate) are invested in a single calf, whereas more resources available to females in Nord-Trøndelag (high twinning rate) are diverted on twins. Ultimately, such differences in the trade-offs between size and fecundity may be an evolutionary product of different mortality patterns (e.g. following different environmental conditions and predation; Proactor et al. 2007). The alternative, i.e. that low calf mass and high twinning rates in Nord-Trøndelag are due to females reflecting previously poor living conditions (e.g. Monteith et al. 2009), is less likely as the population in Nord-Trøndelag has been increasing from low density during the last three decades. Likewise, we find it unlikely that the poor fit between regional mean calf body mass (μ_r) and calf recruitment can be explained by varying perinatal mortality among populations. Indeed, in Oppland, the ovulation rates (proportion ovulating and twin ovulating females) recorded from ovaries, were substantially lower than in Nord-Trøndelag (Solberg et al. 2006, Garel et al. 2009). This suggests that differences in recruitment rates are already settled prior to any calf loss, possibly due to a varying ovulation-to-body-mass relationship among populations (Garel et al. 2009).

Interestingly, the variation in adult sex ratio (females per male) also seemed to affect fecundity as the recruitment rates for a given calf body mass were found to be lower in regions and years with low proportion of adult males (see Table 2). The age and proportion of adult males have decreased substantially in Fennoscandian populations since the introduction of sex and age-specific harvesting in the early 1970s (Nygrén 1987, Lavsund et al. 2003, Milner et al. 2007). Like in other species (e.g. Noyes et al. 1996, Mysterud et al. 2002), such distortions of the population structure can affect reproduction if the number and/or age of males become inadequate to ensure impregnation of all females and/or affects the timing of parturition and hence the size of calves during autumn (e.g. Solberg et al. 2002, Sæther et al. 2004). However, while such a mechanism can explain why we observed a negative effect on the calving rate, it is less clear why the variation in twinning rate is also related to adult sex ratio.

The rate of population increase calculated from life table data is probably the most concise measure of nutritional status or vigour of game populations (Caughley 1977). However, for most species, age-specific fecundity and natural mortality rates are hard to obtain, and for that reason various indices of population nutritional status are often used for monitoring purposes (Hanks 1981). For adaptive management of large herbivores, temporal changes in both population and habitat features, and their interaction, is needed (Morellet et al. 2007, 2011). The twinning rate at birth is one such index that has been used for assessment of moose population nutritional status in North America (Franzmann & Schwartz 1985, Boer 1992, Boertje et al. 2007). Because twins are mainly produced by moose with the highest body mass, age and condition (e.g. Sand 1996, Solberg et al. 2008), the twinning rate at birth is probably a good reflection of the nutritional status in an area. Indeed, the population twinning rate at birth is often found to relate positively to other measurements of population nutritional status (e.g. Boer 1992, Boertje et al. 2007).

In Fennoscandia, aerial surveys of moose reproduction are seldom used for population monitoring, but instead, moose managers utilise recruitment data derived from moose observations by hunters (Morellet et al. 2011). Given that the effect of predation and harvesting is low or can be accounted for, we believe that such data can be used to generate precise indices of population nutritional status. Indeed, as such observations are provided by most hunting teams in Fennoscandia, indices based on a large number of observations can be generated at relatively high spatial resolution. Moreover, because the abundance of wolves *Canis lupus* and bears *Ursus arctos* is still quite modest in Fennoscandia (Swenson et al. 1995, Wabakken et al. 2001, Aspi et al. 2006, Kojola & Heikkinen 2006, Heikkinen et al. 2009, Nygrén 2009), predation is unlikely to have a strong impact on the calving and twinning rates from spring to autumn. An exception is the eastern Finland (Pohjois-Karjala (PK) and Kainuu (KA) in Fig. 1) where large predators are abundant enough to have regional effects on the population productivity of moose (Nygrén 2009).

Biased harvesting of calves and adults may have a stronger effect than predation on the recruitment rates, particularly if the ratio of calves to females in the harvest deviates much from the calf to female ratio in the population (Grøtan 2003). In Fennoscandia, much focus has been directed at harvesting calves and protecting productive females (Lavsund et al. 2003, Nygrén 2009), leading to decreasing calving rates during the hunting season in most populations (Moe et al. 2009). Hence, if the recruitment rates are based on the observations accumulated over the entire hunting season, the recruitment rates are likely to be underestimates. This is in accordance with our results showing that the calf harvest index had a negative effect on the variation in calving rate and twinning rate (see Table 2). This effect seemed to be particularly strong in Norway, probably because of the larger variation in the calf harvest index among Norwegian (range: 0.71-1.62) than Finnish (range: 1.34-1.65) populations.

Based on a simulation study, Grøtan (2003) showed that the variation in calving rate is much more sensitive to variation in the calf harvest rate than is the twinning rate as long as twin calves do not experience substantially higher harvest rates than singletons. This was also supported by our preliminary analyses showing that the twinning rate in Finnish populations did not change much during the hunting season despite substantially higher harvest rates of calves than adult females. The same is likely to be true if predation rates are high and twin calves are not more vulnerable than single calves. In contrast, the observed calving rate may be substantially lower at the end of the hunting season in populations where calves experience high relative harvest rates (or predation rates). Accordingly, the calving rate will probably provide a less precise reflection of the nutritional conditions of a population than do the twinning rate if the variation in calf harvest rate is large and not accounted for. Based on the experience from Finland, such effects of harvesting can best be accounted for by recording the moose observations on a daily basis, from which the pre-harvest calving and twinning rate can be estimated (Nygrén & Pesonen 1993, Nygrén 2009, Morellet et al. 2011).

While the observed twinning rate seemed to be a good index for ranking populations, it showed relatively small variation among years within regions (see Table 1). This is probably due to the resource use tactic found in moose. Although moose females partly rely on ingested food to feed their calves, they are primarily capital breeders (i.e. fecundity is a product of accumulated reserves; Stearns 1992, Jönsson 1997, Mysterud et al. 2005). Accordingly, the number and size of calves is not only a product of the feeding conditions during summer, but also the result of resources accumulated by the mother throughout her life (Keech et al. 1999, Monteith et al. 2009). Such a strategy can partly act as a buffer against short-term environmental effects on the reproductive output making the twinning rate weaker than mean calf body mass in reflecting annual variation in nutritional conditions. In this context, it is also important to note that fluctuations in female age structure (e.g. due to harvesting) may generate variation in twinning rate because older (and larger) moose are more likely to produce twins (Nygrén 1983, 2009). Thus, within a given period, the twinning rate may be high because of high nutritional conditions, high average age of females or both.

For monitoring purposes, we believe that the mean calf body mass is a better index of the short term variation in living conditions than is the twinning rate. Juveniles in ungulates are usually among the first to suffer when the conditions decline (e.g. Gaillard et al. 2000b), and the body mass of calves are found to be closely related to environmental conditions associated with food quality and quantity (e.g. Gaillard et al. 1996 on population density in roe deer, Sæther 1997 in general, Herfindal et al. 2006 for moose), as well as maternal effects (e.g. Keech et al. 1999, Monteith et al. 2009). Moreover, while the mean calf body mass reflects the body condition of one cohort, the observed recruitment rate is a composite of several cohorts that have experienced varying conditions for body growth during life. The observed positive relationship between recruitment rates and calf body mass may therefore mainly reflect that females and calves share similar conditions for body growth and fat accumulation during the summer, which in turn affect female ovulation rates and reproductive rates the next summer. This is in accordance with the result that both the calving rate and twinning rate were best related to variation in mean calf body mass in the previous year and not the current year.

From this perspective, we suggest that the twinning rate is best suited for ranking populations according to nutritional status, as this index is closely related to fitness and is relatively insensitive to variation in perinatal and harvest mortality (see Boertje et al. 2007 for similar conclusions). However, variation in calf body mass may better reflect temporal variation in living conditions. This is because early body growth is sensitive to variation in food availability (and quality) and because body mass responds more instantaneously than recruitment indices to adverse conditions. The earlier response in calf body mass than in recruitment rates also suggests that changes in mean body mass can be used by managers to foresee subsequent changes in recruitment rate. Thus, in absence of more direct censuses prior to the hunting season, the previous year's mean calf body mass can to some extent be used for fine-tuning hunting quotas and to reduce the time lag often found between changes in resource abundance and management decisions (Fryxell et al. 2010).

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