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Fitness consequences of selection of home range in moose (*Alces alces*)

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Biology

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Abstract

The body mass in early life can have great impact on lifetime fitness in ungulates. In this study, I examined how maternal effects and home range quality affect calf body mass in a moose population on the island of Vega in northern Norway. For this I used data from 23 adult female moose that produced 87 calves during 11 years (in total 54 moose-years).

I found that the calf body mass was related to maternal characteristics, as well as habitat qualities in the home range of the mother. The body mass of the calf was positively related to the age of the mother, probably because older mothers have higher body condition and more experience. In addition, I found the body mass of calves to be larger when the home range of the mother had a high proportion of the most selected habitat types (“agriculture” and “fair” habitats) than when it was dominated by the least selected habitat types (“poor” habitats).

Interestingly, I found no effect of the home range composition on the calf body mass recorded at the end of summer, the effect first became visible in calves measured in winter. Possible explanations for this may be that the mother’s milk production is of most importance for the calf’s body growth during summer, or that the foraging conditions during summer are too favourable to give rise to any detectable variation in body mass in autumn.

The effects of the mother’s age and the habitat composition of her home range remained significant when combined in the same statistical models. This indicates that the quality of the home range and the age and experience of the mother have additive effects on the variation in calf body mass at Vega.

Because body mass in early life have long lasting effects in ungulates, the moose calves born from an experienced mother that inhabits a favourable home range are expected to have a higher lifetime reproductive success at Vega. Although several studies have documented fitness consequence of habitat utilisation, few studies have documented that such habitat effects on life history traits can occur already during the first year.

Sammendrag

Kroppsmassen tidlig i livet kan ha stor innvirkning på livstidsfitness hos hjortedyr. I dette studiet undersøkte jeg i hvilken grad maternale effekter og habitatkvaliteten i leveområdet påvirker variasjonen i kalvevekt i en elgbestand på øya Vega i Nord-Norge. Jeg undersøkte data fra 23 voksne elgkyr som produserte 87 kalver i løpet av 11 år (totalt 54 elg-år).

Jeg fant at kalvens vekt var relatert til egenskaper ved mora, samt til habitatkvaliteter i leveområdet til mora. Kalvevekta var positivt relatert til moras alder, sannsynligvis fordi eldre mødre er i bedre kondisjon og er mer erfarne. I tillegg var kalvevekta høyere når leveområdet til mora hadde en høy andel av de mest selekterte habitattypene ("agriculture" = jordbruksland, og "fair" = middels gode habitat) enn når det var dominert av mindre selekterte habitattyper ("poor" = fattige habitat).

Et interessant funn var at leveområdets habitatsammensetning ikke påvirket kalvens høstvekt, men kun kalvenes vintervekt. Mulige forklaringer på dette er at variasjonen i moras melkeproduksjon er av størst betydning for kalvens vekst i løpet av sommeren enn variasjonen i habitatsammensetningen, eller at beiteforholdene i sommersesongen er generelt for gode til å påvirke vektvariasjonen på høsten.

Effekten av moras alder og effekten av habitatsammensetningen innenfor leveområdet forble signifikante når begge ble inkludert sammen i statistiske modeller. Dette antyder at kvaliteten på leveområdet og mors alder og erfaring har additive effekter på variasjonen i kalvevekt på Vega.

Fordi kroppsveksten tidlig i livet er positivt assosiert med størrelsen som voksen, forventer jeg at elgkalver født av erfarende mødre i matrike leveområder, vil ha jevnt over høyere reprodutiv suksess i løpet av livet. Mens flere studier har vist at kvaliteter i hjemmeområdet påvirker fitness, er det imidlertid få studier som har vist at slike habitateffekter kan oppstå allerede tidlig i livet.

1. Introduction

The role of individual variation on population dynamical processes has currently received increased attention (Vindenes et al. 2008; Steiner and Tuljapurkar 2012). In order to fully understand such processes, we need knowledge about the factors that generates these variations (Beckerman et al. 2006). Direct and immediate effects of climate and density on individuals life history traits are well understood in many species (e.g. ungulates: Gaillard et al. 2000). Another source of variation in individual performance is conditions experienced early in life (Lindström 1999), which often lasts into adulthood (Solberg et al. 2004; Solberg et al. 2008), and generates persistent individual differences in lifetime performance (Gaillard et al. 2003; van de Pol et al. 2006). It is therefore important to understand factors causing individual differences in early life (Beckerman et al. 2003).

Whereas the role of temporal variation in environmental conditions on life history traits of juveniles have received considerable attention (e.g. Herfindal et al. 2006), the role of maternal factors and effects of resource availability and utilization is less known. In ungulates, it is generally assumed that females reproductive performance increase with age until senescence (Loison et al. 1999). Moreover, offspring body mass is found to be positively related to the body mass of the mother. However, availability of high-quality resources is also important, and access to such at early stages can be a silver spoon with respect on future reproductive performance (van de Pol et al. 2006). In ungulates, this can operate both indirectly through lactation and directly through the shared resources with the mother. Consequently, maternal effects and habitat effects can be hard to separate, because mother's condition can be a correlate of her choice of habitats.

The positive relationship between body mass and vital rates is well documented among ungulates (Sæther 1997; Gaillard et al. 2000). Moose (*Alces alces*) body mass is important for e.g. age of maturity (Sand 1996; Sæther and Heim 1993), reproductive success (Sand 1996; Solberg et al. 2004; Sæther 1997) and longevity (Keech et al. 2000). Individual differences in body mass as calf (<1 year old) often last until adulthood (Solberg et al. 2004; Solberg et al. 2008; Sæther et al. 2003), although with varying strength depending on sex and age (Solberg et al. 2004). Because the body mass in early life is important for later development and fitness, it is important to identify factors contributing to the variation in body mass of calves.

Access to forage, both in quantity and quality, is important for moose development and reproduction (Andersen and Sæther 1992). Studies have suggested that quality rather than quantity of food is of most importance, both during summer (e.g. Herfindal et al. 2006) and winter (e.g. Andersen and Sæther 1992). Therefore, a large proportion of the variation in calf body mass is expected to be affected by the availability of high quality forage in the home range of the calf. Habitat components important for the selection of home range in large herbivores are for instance food and cover (McLoughlin et al. 2007). Home range size in ungulates can vary greatly within a population, as for instance were found in a roe deer (*Capreolus capreolus*) population where the home range sizes varied by up to three orders of magnitude between and within individuals, possibly because of varying habitat quality within home ranges (Harestad and Bunnell 1979; Börger et al. 2006b). In ungulates, females with calves have also been found to move into suboptimal habitats, possibly to reduce the predation risk of their offspring (e.g. Grignolio et al. 2007).

The phenotype of an individual may be affected by its genotype and its environment, as well as by maternal effects. Maternal effects are non-genetic correlations between the calf's phenotype and the mother's phenotype and/or her environment (Mousseau and Fox 1998). Reproduction is energetically demanding and a mother only has a certain amount of resources to allocate to her offspring (Clutton-Brock et al. 1989; Sand 1998). Several ungulate studies have shown a positive relationship between the mother's body condition and the offspring phenotypic quality (e.g. Côté and Festa-Bianchet 2001; Keech et al. 2000; Solberg et al. 2007). In moose, the condition of the cow can affect the calf body mass at birth (Keech et al. 2000), as well as after birth, for instance due to varying milk production (Sand 1998; Solberg et al. 2004). Accordingly, the moose calf body mass have been shown to increase with the body condition and/or age of the mother (Sæther et al. 2001; Solberg et al. 2007). In addition, there are some indications that the calf body mass can be related to the quantity and quality of food available in the mothers' home range (Sviland 2001; Sæther et al. 1996).

When investigating the effects of home range quality on calf fitness (e.g. body mass) it is difficult to separate habitat from maternal effects. However, if the maternal effects, e.g. through mother age, body size and date of birth are known, they can be controlled for when investigating the effects of home range quality on offspring fitness. However, the expected relationship between the body mass of calves and home range quality may still not be found because of the density and distribution of individuals between habitats (McLoughlin et al.

2006). Indeed, many studies have shown that population density influences the development and reproduction in large ungulates (e.g. Ferguson et al. 2000; Herfindal et al. 2006; Pettoirelli et al. 2001; Sæther 1997), for instance due to food competition (Skogland 1983).

In this study I examined to what extent habitat qualities in the mother's home range, as well as maternal conditions, can explain parts of the variation in calf body mass in moose. I did this at the island of Vega, located off the coast of Helgeland in northern Norway. Vega measures about 119 km², of which about 80 km² is considered suitable moose habitats (Solberg et al. 2010). The small size gives all moose the opportunity to learn about the available resources of the island, and because moose are not territorial animals, all individuals should be free to utilize the habitats where they will do best. The island is relatively isolated with few moose migrating to or from the study area (Solberg et al. 2010).

Moose habitat selection and environmental impact on moose body mass have previously been studied on Vega by Herfindal et al. (2009) and Sviland (2001). Herfindal et al. (2009) found that the moose generally preferred habitats with good foraging conditions and cover and tried to avoid human disturbed areas. The results were however scale dependent, showing that cover and forage were of most importance on the landscape scale (selection of home range) while perceived mortality risk was the most important factor determining habitat selection within home ranges. Accordingly, Herfindal et al. (2009) suggested that home range size at Vega was a function of individual energetic demands and forage availability, as well as the distribution of protective cover and human impact. The results of the study did not support the hypothesis of density dependent habitat selection, assumingly because of low population density (Solberg et al. 2010), good foraging conditions on the island (Solberg et al. 2008) and a resulting high growth rate in the population (Sæther et al. 2007).

When investigating the effect of home range quality on moose body mass at Vega, Sviland (2001) found no significant correlation between the body mass of the cows and calves and the size of the home range. However, a large proportion of the variance in calf weights could be explained by the variance in mother body mass and by the presence of vegetation types with high food production in the summer home range. However, as there was a correlation between the body mass of the mother and that of the calf (Olstad 2000), and the mother's body mass was correlated with the home range (Sviland 2001), the effect of home range quality on the calf weight may not be independent of maternal effects.

In this project I took the advantage of the results from Herfindal (2009) and Sviland (2001) on habitat utilization, home range quality and fitness related traits of moose at Vega. I then investigated if calf body mass depends on maternal effects and on the habitat composition of the mother's home range with respect to habitat types that are selected for or avoided by moose in the populations (Herfindal et al. 2009). I predicted that calf body mass, when accounting for individual characteristics such as birth date and number of siblings, is positively related to mother's conditions such as body mass and age (maternal effects). In addition, I predicted that the home range quality of the mother affect the body mass of her calves. Specifically, I predicted that calf body mass is positively related to the availability of preferred habitat types in the mother's home range, and negatively related to habitat types that are commonly avoided by moose. Finally, I investigated whether the effect of habitat operates through the maternal effect, i.e. that there is a correlation between mothers age or body mass, and the habitat composition of her home range. If so, I predicted that when including maternal factors and habitat composition in the same model, calf body mass will show little or no relationship with one of the aforementioned variables. In contrast, if mother's age and body mass are unlinked to the quality of her habitat, I predicted that maternal and habitat effects remain significant correlates of calf body mass when included in the same model.

2. Material and methods

2.1 Study area and habitat classification

The study area is at the island of Vega (65°40'N, 11°55'E) located off the coast of Helgeland in northern Norway (Figure 1), about 30 km from the mainland (Sæther et al. 2004). The island measures about 119 km². The climate is oceanic, with relatively cool and wet summers (mean temperature 13 ± 3 °C) and mild winters (0.5 ± 4 °C; Tremblay et al. 2007). Snow covers the ground only a few days during winter, and the snow depth is generally low (Solberg et al. 2011). This type of climate is favourable for plant growth because it gives a relative high sum of temperature and a long growing season (Angeloff et al. 2004).

The south-western part of Vega is dominated by a mountainous landscape, which is mostly inaccessible and not used by moose, leading to about 80 km² of the island as suitable moose habitat (Solberg et al. 2010). Except for the mountain area, the landscape on the islands is

relatively flat. A detailed vegetation analysis of the island was made in 2000 and 2003 (Angeloff et al. 2004), providing a good overview of the quality and quantity of the potential moose food on Vega. The dominating coarse vegetation types is moorland (32%), forests (15%, with Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and birch *Betula pendula* and *B. pubescens*), marshes (12%), agricultural areas (mainly for grass production, 13%) and grassland (8%)

Following Herfindal et al. (2009), I used a classification of the vegetation that focuses on the value of the vegetation as forage for cattle. Although cattle and moose to some extent differ in their foraging niche, there is a high level of overlap particularly during summer (see references in Herfindal et al. 2009). I did not separate the vegetation types according to forest cover, because I was mainly interested in the role of forage quality, and not cover which only have a minor role in the predator-free environment at Vega. I chose to assess the importance of the habitat types "poor", "fair", and "agriculture" (see below). The choice of these habitat types was based on an overall evaluation of how moose selected these at the landscape (home range habitat composition vs. island composition) and home range level (habitat of use vs. home range composition). Fair habitat ranges was selected by moose at the home range level, whereas poor areas were avoided when open, and preferred when closed (forest) at both spatial scales (Herfindal et al. 2009). Agricultural areas were highly preferred at the landscape level, but avoided at the home range level (Herfindal et al. 2009). The latter result is probably caused by the fact that all moose locations were recorded during the day (Herfindal et al. 2009), and that moose during summer tend to utilise agricultural areas during the night (Bjørneraas et al. 2011). Other habitat types were omitted, either because they covered only small parts of the island, or because they were mostly unrelated to moose foraging conditions and therefore not considered moose habitat (e.g. developed areas and bare rock).

Poor habitats were dominated by tundra, wet alpine meadows, bogs (forested and unforested) and heather moors, and pine forest dominated by lichen or heather as ground cover (Angeloff et al. 2004). Fair habitats were dominated by grassy vegetation types (alpine meadows, grassy bogs and swamps) and forests with bilberry or pastures (Angeloff et al. 2004). Agriculture habitats were fields for grass production.

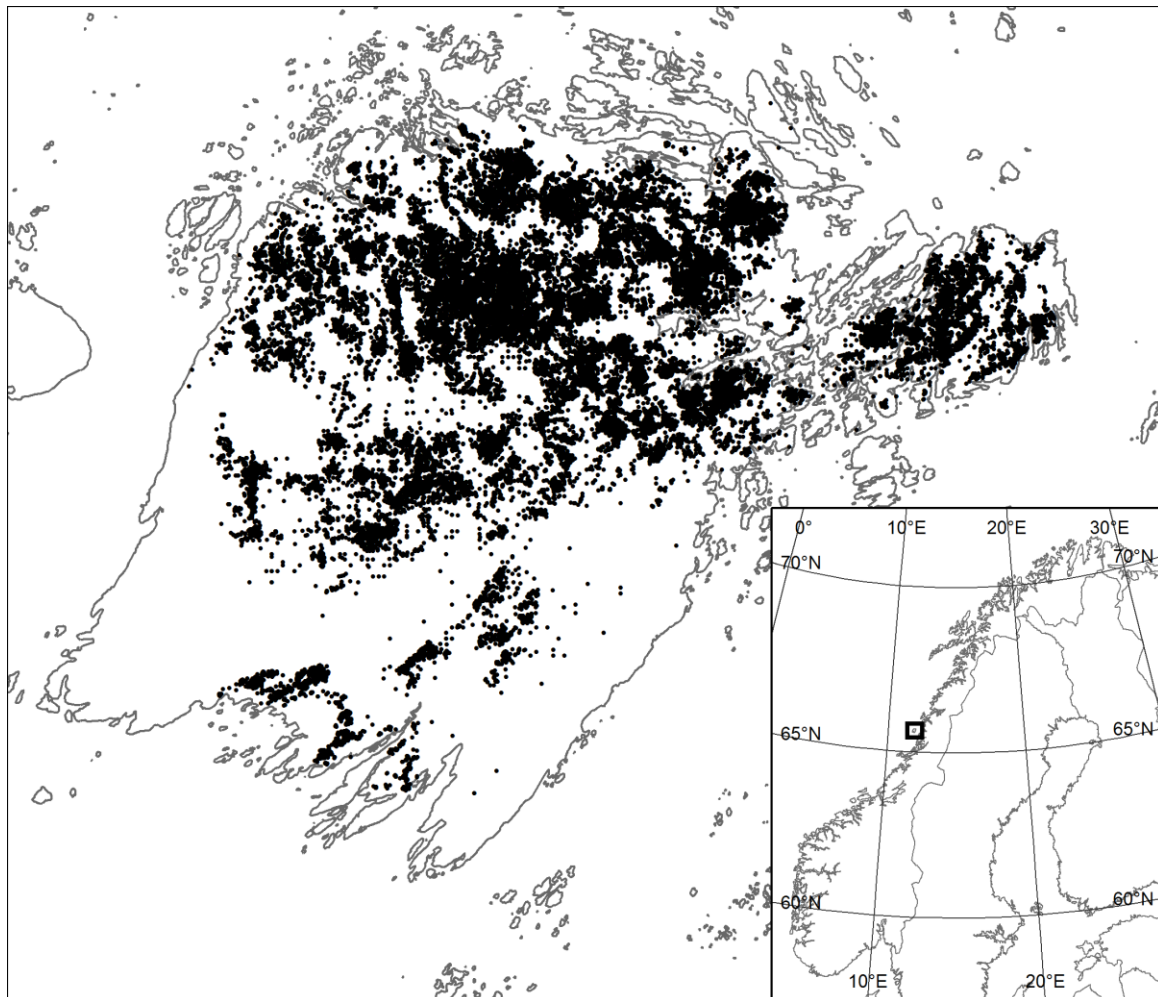


Figure 1 The study area: the island Vega. Black dots indicate the locations of VHF- and GPS-collared female moose used in the study. The white areas in the south-west and south-east of the island are steep and mountainous and considered unsuitable for moose.

2.2 Moose data

Since 1992, NINA has conducted several moose projects on Vega, which makes the moose population a well-known study system (Solberg et al. 2010; Solberg et al. 2011). In 1992 and 1993, all moose on the Island were first captured and radio-collared (for capture protocol details, see Solberg et al. 2011). The following winters (January-March), close to all (> 95%, Solberg et al. 2011) new calves from around 8 months of age surviving the previous hunting season have been radio-collared (Solberg et al. 2011). Also immigrants have been radio-collared, and individuals with malfunctioning radio-transmitters or lost collars have been re-collared (Solberg et al. 2011; Sæther et al. 2007). During the collaring process, the body mass of most animals were measured to the nearest kilogram (± 2 kg) by a scale installed in or hanging from the helicopter (Solberg et al. 2008).

Age of individuals captured as calf was determined as the time passed since collaring. For individuals born before the start of the study period or that otherwise were not collared as calves (e.g. immigrants), age determination was done by counting the number of layers in the secondary dentine of the incisors (Rolandsen et al. 2008) after the moose was killed in the autumn hunt or found dead due to other causes. During the calving season (May-June) the females were approached by foot every 3-4 days until calving (Tremblay et al. 2007), and the date of birth was estimated with high precision (for more details about the procedure, see Sæther et al. 1996). In addition, the number and sex of the calf/calves following the cow were determined by visual observations during summer or early autumn (Sæther et al. 2001).

The natural mortality rates of moose are generally low at Vega (approximately 2%; Solberg et al. 2011) compared to other populations in Northern Norway (approx. 5%; Solberg et al. 2005; Stubsjøen et al. 2000). There are no large predators on the Island, and the only potential predators on moose calves are eagles and stray dogs (Solberg et al. 2011). Hunting is the main cause of mortality (Sæther et al. 2003), and since 1995 the estimated winter population size has been kept low within the range of 28-37 animals (Solberg et al. 2010). During the annual hunting season on Vega (25th September - 31st October), the carcass mass (body mass after removal of the head, skin, metapodials, bleedable blood and viscera, approximately 50-56% of total body weight) of harvested animals have been recorded by local hunter groups (Solberg et al. 2008).

Throughout the year, moose marked with Very High-Frequency (VHF)-collars were periodically relocated from the ground by radio-triangulation on a grid with 100 m resolution (Sæther et al. 2001). Most effort in relocating the animals was put in the calving season (May-June), late summer (July/August) and in the rutting season (September-October) (Sæther et al. 2001). Later in the study period the animals were equipped with Global Positioning Systems (GPS)-collars, programmed to obtain locations at 1 or 2 hours interval.

2.3 Home range analysis

When estimating home ranges, a systematic sampling protocol that does not differ much among individuals is preferred to avoid biases in home range estimates and effects of autocorrelation among observations (Otis and White 1999). The VHF-data varied in sampling frequency both within and among individuals. I therefore followed the sub-sampling protocol

by Herfindal et al. (2009) to obtain VHF data that was fairly systematic. Observations were sampled from 1st of May to 30th of September. GPS data were screened for location errors by the method developed by Bjørneraas et al. (2010). This method takes into account the behaviour of the moose and removes obvious location errors (Bjørneraas et al. 2010). The remaining GPS positions from the summer season (1st of May – 30th of September) were all included in the home range analyses. Whether the cow was VHF or GPS collared was assumed to have no effect on the estimated home ranges.

As home range is a biological concept, it is argued that no home range estimator can reflect the true home range of an animal (Kie et al. 2010; Laver 2005). The choice of home range estimator should depend on the objective of the study, the nature of the data, and movement behaviour of the study animal (Laver 2005). In this study, two different home range estimators were used to account for possible limitations with the estimators (e.g. Börger et al. 2006a; Nilsen et al. 2008).

I used 95% minimum convex polygon (MCP) and 95% kernel density estimate (KDE) to delineate the moose home range. The 95% MCP delineates the home range border along the outermost points, where 5% of the points farthest away from the arithmetic mean are removed to reduce impact of excursions and outlier observations. KDE utilises all observations and generates a density distribution of moose occurrences based on the spatial distribution of the locations. Areas with high density of points will have high probabilities. I used a fixed smoothing bandwidth of 300 m, and extracted the 95% probability contour as the KDE home range. The bandwidth was subjectively chosen based on a preliminary examination of the location data distribution and knowledge about moose behaviour. Home ranges were calculated with the package `adehabitatHR` (Calenge 2006) in the R software (R Development Core Team 2011).

In total, 54 estimated summer home ranges were included from 23 cows (17 VHF- and 6 GPS-collared), for which I also had data recorded about her calf/calves ($n = 87$) the corresponding year. Eleven years were represented from the study period (years 1993-1997, 2004-2007, and 2009-2010). The composition of habitat types within home ranges was calculated by overlaying the home ranges with the habitat map in ArcGIS Editor Version 9.3 (ESRI 2010). For each home range I had the proportion of each of the three habitat types,

calculated as area of the specific habitat type divided by the home range size (where the part of the home ranges that were in the sea was excluded).

2.4 Statistical analysis

The calves' body masses were measured either as carcass mass in autumn or live body mass in winter. I kept the two weight categories separated throughout my statistical analyses by adding weight type as a covariate in all models. Variation between years, for instance because of climatic conditions (which may give rise to variation in forage quality between years), moose density and cohort effects, was controlled for by the use of linear mixed models (LME) with year as a random factor in all models. I also had repeated measures per individual cow and per year in my data. However, any interdependence in observations due to several observations per cow was expected to be captured by the individual and habitat characteristics of the cow, and I therefore did not include cow as a random factor in the analyses. I used Akaike Information Criterion (AIC) for small sample sizes (AICc) to rank candidate models, and the models with the lowest AICc score was considered to be the most parsimonious (Burnham and Anderson 2002).

Based on previous studies (see Introduction), I expected the calf body mass to be related to the calf's sex, number of siblings, age (i.e. measured in autumn or winter), and the date of birth (e.g. because calves born early in spring have access to fresh vegetation for a longer period). The calves are expected to still gain weight during the hunting season, and lose weight in the course of the winter due to harsher climatic and foraging conditions. I therefore expected contrasting effects of birth date on body mass in autumn (carcass mass) and winter (live body mass).

Table 1 summarised how body mass was related to other characteristics of the calves. I adjusted the carcass mass and live body mass of the calves according to the parameter estimates in Table 1 such that each body mass represented the carcass mass/live body mass of a single, male calf, with a given birth date (the mean birth date: May 25th), at a given age (137 days old for carcass mass, 258 days old for live body mass), and for a given weighting date in autumn (the mean date for measure of carcass mass: October 8th) or winter (the mean date for measure of live body mass: February 6st).

Table 1. Parameter estimates and standard errors for the effects of calf characteristics on its body mass. The parameter estimates was used to adjust calf body mass to represent a single male calf with a given age and birth date (carcass and capture body mass held separated). Weight type is winter live body mass (intercept) or autumn carcass mass. 95% confidence interval was calculated based on 10,000 resamplings from the posterior distribution of the parameter estimates (for details, see Material and Methods, Statistical analyses).

Variable	β	\pm SE	95% CI
Intercept	319.85	50.18	220.21; 417.53
Sex (male)	14.85	3.67	7.59; 22.09
Weight type	-314.11	129.45	-568.83;-55.86
Weight day number	-0.32	0.16	-0.62; 0.00
Birth date	-0.86	0.35	-1.51; -0.14
Number of siblings	-2.66	4.21	-11.73; 5.23
Sex male \times weight type	-7.80	5.84	-19.58; 3.55
Weight type \times weight day number	0.78	0.39	-0.01; 1.52
Weight type \times birth date	0.46	0.47	-0.51; 1.39

Having controlled for the above factors, I expected that the remaining variation in calf body mass to a large extent would be the result of maternal effects and/or habitat effects. The maternal effect on calf body mass was first analysed in “maternal effects” models using linear mixed models with year as random factor. Data on mother mass was lacking for most calves included in my analyses, and because of low statistical power this variable was not included in my analyses. The full maternal effects model included the parameters mother age, the timing of birth (because cows in good condition may be able to give birth earlier in spring than cows in poorer condition), weight type, and the interaction term between mother age and weight type (to see if an impact of mother age on calf body mass differed between calves measured in autumn and winter).

When testing for effects of home range characteristics on calf body mass (Table 4), models were run separately with habitat composition based on KDE and MCP. The effect of the availability of the three habitat types on calf body mass were analysed in separate models. The full “habitat effects” models included the main effects of home range size and of the proportion of the habitat type of interest, together with their interaction term. The interaction term was included to see if the effect of habitat changed with the size of the home range. For

instance, a significant interaction between proportion available habitat and home range size would indicate that it was the absolute area (proportion of a habitat multiplied with total home range size = total area of the habitat) rather than the proportion available that was important for calf body mass. The habitat models also included the parameter weight type and the interaction term between weight type and habitat proportion, to investigate if the habitat had different effect on the calves' carcass masses in autumn and live body mass in winter.

In the final step, I combined the variables from the best "maternal effects" model and the best "habitat effects" models in a "combined maternal and habitat effects"-model. This allowed me to investigate whether the maternal effect was still important when the home range characteristics were taken into account, and opposite; whether the effects of the habitats were important when accounting for maternal effects. The interaction term between mother age and proportion of the respective habitat types was included to assess whether the effect of the habitat changed with mother age.

All statistical analyses were performed using R version 2.14.0 (R Development Core Team 2011) with the package lme4 (Bates et al. 2011) used for linear mixed models analyses. The 95% CI for the parameter estimates was based on 10,000 resamplings from the posterior distribution of the parameter estimates from the fitted model by the functions mcmcSamp and HPD interval.

3. Results

3.1 Calf characteristics

The calves' carcass masses in autumn varied from 58 to 100 kg with a mean of 78 kg (n = 31). Live body mass in winter varied between 145 and 222 kg with a mean of 191 kg (n = 56). Examining calf body mass variation in relation to sex and litter size showed that males (n = 46) were on average 14.85 ± 3.67 kg heavier than female calves (n = 41) in winter, while twin calves (n = 75 individual calves) were non-significantly smaller (-2.66 ± 4.21 kg) compared to single calves (n = 12) (Table 1). All calves included in my study were born during a 30 day-period, starting in mid-May and ending in mid-June. Being born later in the calving season had a negative effect on the calf body mass; the winter live body mass decreased with 0.86 ± 0.35 kg per day with increasing date of birth (Table 1). Carcass mass increased with date of

kill (0.46 ± 0.16 kg per day, Table 1), indicating that calves still gained weight during autumn. For live body mass measured during the collaring period in winter, there was a weak, non-significant decrease (-0.32 ± 0.16 kg, Table 1) in body mass with increasing date of collaring.

3.2 Maternal effects on calf body mass

The mothers ($n = 23$) included in my analyses ranged from 2 to 13 years of age, with a mean age of 6 years. The maternal model explaining variation in calf body mass that achieved the lowest AICc-value included mother's age and weight type, but not birth date or the interaction between mother's age and weight type (Table 2). The second best model also included the interaction between mother age and weight type, and had a $\Delta AICc$ of 0.99. Hence, this model provides as good fit to the data as the highest ranked model. Still, I chose the simpler model over the complex. The highest ranked model (Table 2) suggested that calf body mass increased with increasing mother age, and this relationship was the same for both carcass mass in autumn and live body mass in winter (Table 3, Figure 2).

Table 2. AICc-based ranking of models explaining the variation in calf body mass by maternal effects. An X indicates that the variable was included in the model. Only the five highest ranked models are given. Models are fitted as linear mixed models with year as random factor. An x indicates an interaction between the variables. Models with interaction terms always include the main factor of both variables.

	Birth date	Mother age	Weight type	Mother age × weight type	AIC _c value	ΔAIC _c	AIC _c weights
1		X	X		685.42	0.00	0.404
2		X	X	X	686.41	0.99	0.246
3	X	X	X		686.75	1.33	0.207
4	X	X	X	X	687.85	2.43	0.120
5			X		691.79	6.37	0.017

Table 3. Parameter estimates \pm SE, (95% confidence interval) from the highest ranked models explaining the variation in calf body mass with respect to maternal effects. Weight type is winter live body mass (intercept) or autumn carcass mass. 95% confidence interval was calculated based on 10,000 resamplings from the posterior distribution of the parameter estimates (for details, see Material and Methods, Statistical analyses).

Variable	β	\pm SE	95% CI
Intercept	189.87	3.62	182.38; 196.93
Mother age	1.59	0.54	0.55; 2.69
Weight type	-115.72	2.85	121.13; -0.109.78

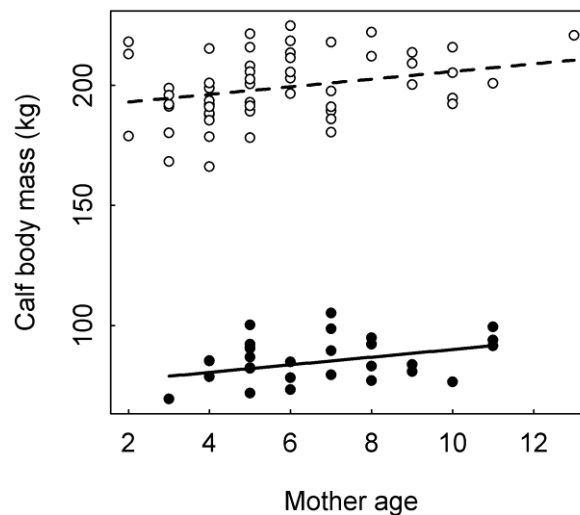


Figure 2. Variation in calf live body mass (kg) in winter (*open circle*) and carcass mass in autumn (*closed circles*) in relation to the mother age (years). Lines indicate predicted relationships based on parameter estimates in Table 3.

3.3 Habitat effects on calf body mass

The highest ranked models of habitat effects on calf body mass did not differ much between models using home ranges based on KDE or MCP. The general pattern was that the MCP-models were somewhat simpler (e.g. for the effect of fair habitat), but the general conclusions did not depend on the choice of home range estimator. Because the MCP-models were simpler and thereby more conservative, I chose to focus on these. However, I also provide model evaluation and parameter estimates from KDE-models in tables 4 and 5. All selected best models from analysing the effect of home range characteristics included home range size as a variable in explaining the variation in calf body mass (both carcass mass and live body

mass) (Table 4). The home range size effect was either non-significant or significantly negative in all models, indicating that the calf body mass decreased when the home range increased in size (Table 5).

In the analyses of the relationship between calf body mass and proportion agriculture habitat in the home range, the best model based on MCP included proportion agriculture area, home range, sex, weight type and the interaction between proportion agriculture and weight type (Table 4A). Two alternative models, both including the interaction between home range size and proportion agriculture areas had relatively low ΔAICc , indicating support also for these models (Table 4A). Still, I chose the simpler model over the more complex models. According to this model, there was a positive relationship between the proportion of agriculture habitat on winter live body mass, but not on autumn carcass mass (Table 5A, Figure 3A).

The highest ranked MCP-model for the effect of fair habitat on calf body mass included home range size, proportion fair habitat, weight type and the interaction between proportion fair habitat and weight type (Table 4B). The alternative full model had a ΔAICc of 0.67, which indicates that also this model was a good model. I favoured the simpler model over the more complex one, and this model predicted that calf winter body mass increased with increased proportion of fair habitat in the mother's home range, but no effect on carcass mass (Table 5B, Figure 3B).

The highest ranked poor habitat model (based on MCP) included home range size, proportion poor habitat, weight type and the interaction between weight type and proportion poor habitat (Table 4C). The full model had a ΔAICc of 0.59, whereas other alternative models had $\Delta\text{AICc} > 2$. The highest ranked model showed that winter body mass was negatively related to the proportion poor habitat in the summer home range of the mother, but no effect on the autumn carcass mass (Table 5C, Figure 3).

Table 4. AICc-based ranking of models explaining the variation in calf body mass in relation to habitat composition of the mother’s home range. An X indicates that the variable was included in the model. Only the five highest ranked models for each habitat type and home range estimator are given (MCP = 95% minimum convex polygon, KDE = 95% kernal density estimator). Models are fitted as linear mixed models with year as random factor. An x indicates an interaction between two variables. Models with interaction terms always include the main factor of both variables.

		HR size	Prop. habitat	Weight type	HR size × prop. habitat	Prop. habitat × weight type	AIC _C value	ΔAIC _C	AIC _C weight	
A	Agriculture habitat	1	X	X	X		684.14	0.00	0.291	
		2	X	X	X	X	684.37	0.23	0.260	
		MCP	3	X	X	X		684.41	0.27	0.255
		4	X	X	X			686.36	2.22	0.096
		5		X	X		X	687.10	2.96	0.066
	1	X	X	X		X	683.33	0.00	0.405	
	2		X	X		X	684.11	0.78	0.275	
	KDE	3	X	X	X	X	685.10	1.77	0.167	
	4	X	X	X			686.74	3.31	0.074	
	5		X	X			687.67	4.34	0.046	
B	Fair habitat	1	X	X	X		682.82	0.00	0.386	
		2	X	X	X	X	683.43	0.62	0.283	
		MCP	3		X	X		683.78	0.97	0.238
		4	X	X	X			687.52	4.70	0.037
		5		X	X			688.48	5.66	0.023
	1	X	X	X	X	X	689.46	0.00	0.300	
	2	X	X	X	X		690.95	1.50	0.142	
	KDE	3	X	X	X		691.16	1.70	0.128	
	4		X	X		X	691.56	2.10	0.105	
	5			X			691.79	2.33	0.094	
C	Poor habitat	1	X	X	X		680.38	0.00	0.474	
		2		X	X		X	680.97	0.59	0.353
		MCP	3	X	X	X	X	682.79	2.41	0.142
		4	X	X	X			687.25	6.88	0.015
		5		X	X			689.21	8.83	0.006
	1	X	X	X	X		688.89	0.00	0.272	
	2	X	X	X	X	X	689.20	0.31	0.233	
	KDE	3		X	X		X	690.76	1.87	0.107
	4		X	X			690.78	1.89	0.106	
	5	X	X	X		X	690.95	2.06	0.097	

Table 5. Parameter estimates \pm SE, (95% confidence interval) from the highest ranked models explaining the variation in calf body mass by the proportion of different habitat types in their home range. MCP and KDE indicate whether mother's home range was estimated using 95% minimum convex polygon or 95% kernel density estimator, respectively. Weight type is winter live body mass (intercept) or autumn carcass mass. 95% confidence interval was calculated based on 10,000 resamplings from the posterior distribution of the parameter estimates (for details, see Material and Methods, Statistical analyses).

		Intercept	HR size	Prop. habitat	Weight type	HR size \times prop. habitat	Prop. habitat \times weight type
A Agriculture habitat	M C P	190.73 \pm 4.44, (181.72; 199.43)	-0.49 \pm 0.22, (-0.93; -0.06)	92.00 \pm 27.32, (40.11; 148.01)	-101.55 \pm 6.30, (-114.47; -88.76)	-	-87.37 \pm 41.84, (-172.89; -5.22)
	K D E	182.24 \pm 6.91, (168.88; 196.57)	-0.53 \pm 0.31, (-1.15; 0.07)	178.16 \pm 47.45, (83.52; 273.08)	-92.52 \pm 9.64, (-111.06; -72.55)	-	-167.16 \pm 70.95, (-315.59; -33.22)
B Fair habitat	M C P	190.24 \pm 4.42, (181.72; 198.93)	-0.37 \pm 0.21, (-0.80; 0.03)	60.95 \pm 16.91, (26.64; 94.06)	-100.84 \pm 6.09, (-112.83; -88.81)	-	-64.62 \pm 24.15, (-112.06; -16.21)
	K D E	171.54 \pm 12.51, (146.60; 195.81)	1.78 \pm 1.20, (-0.56; 4.18)	145.15 \pm 52.34, (43.49; 251.07)	-101.15 \pm 7.49, (-115.26; -85.28)	-9.77 \pm 4.90, (-19.33; -0.01)	-56.37 \pm 29.02, (-115.96; -1.12)
C Poor habitat	M C P	230.33 \pm 7.64, (214.30; 244.70)	-0.35 \pm 0.21, (-0.79; 0.04)	-58.18 \pm 14.79, (-87.59; -28.42)	-146.29 \pm 10.74, (-167.24; -124.44)	-	67.47 \pm 22.09, (24.51; 113.34)
	K D E	263.36 \pm 23.05, (217.20; 308.93)	-4.98 \pm 2.10, (-0.29; -0.90)	-131.14 \pm 49.51, (-224.54; -27.84)	-115.18 \pm 2.87, (-120.67; -109.33)	10.09 \pm 4.57, (0.73; 18.93)	-

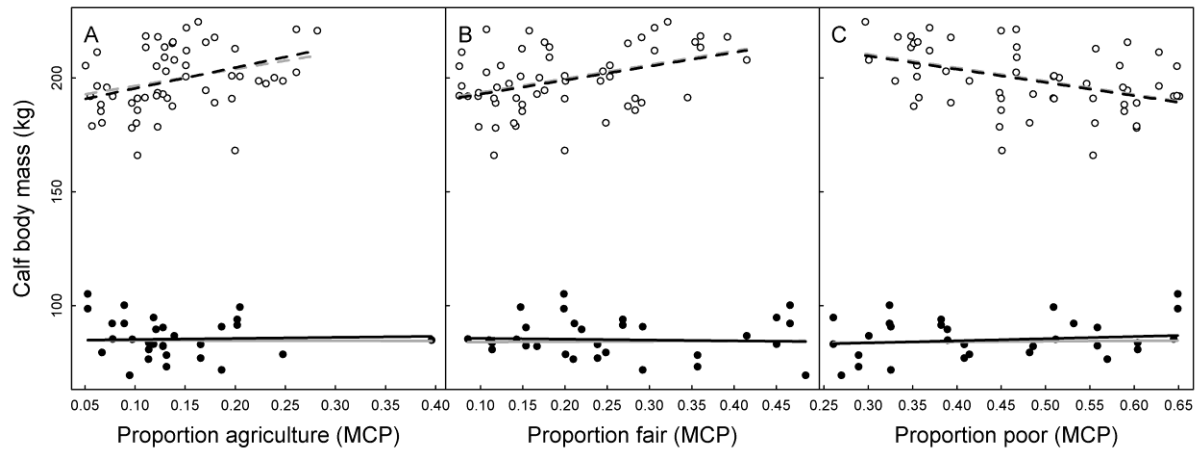


Figure 3. Variation in adjusted calf live body mass (kg) in winter (*open circles and dashed lines*) and carcass mass in autumn (*closed circles and solid lines*) in relation to the proportion of agriculture areas (A), fair habitat (B), and poor habitat (C) in mother's summer home range. Black lines indicate predicted relationship based on parameter estimates from the highest ranked habitat models (Tables 4 and 5), whereas grey lines are the predicted relationship while also accounting for mother's age (i.e. the highest ranked combined models, Tables 6 and 7). Note that the two lines nearly overlap.

3.4 The combined maternal and habitat effects on calf body mass

As for the habitat models, there were only minor differences between MCP-based and KDE-based models, where KDE-models were somewhat more complex. I therefore chose to focus on MCP-models also when assessing the combined maternal and habitat effects on calf body mass, but refer to Tables 6 and 7 for results on KDE.

The best maternal-agriculture model included all variables from the best maternal model and the best agricultural model (Table 6A). This model had an AICc value 1.25 lower than the best alternative models, which did not include the interaction between proportion agricultural area and weight type. Other alternative models had $\Delta\text{AICc} > 2$. The highest ranked model confirmed the results both from the best maternal model, i.e. increased calf body mass with increasing age, and the best agricultural model, i.e. positive relationship between proportion agricultural areas and winter calf body mass, but not autumn carcass mass, Table 7A.

Also for the model including maternal effect and proportion fair habitat, the highest ranked model included mothers age, weight type, home range size, proportion fair habitat and the interaction between weight type and proportion fair habitat (Table 6B). Alternative models had $\Delta\text{AICc} > 2$. Again, the highest ranked model confirmed the positive relationship between

mothers age and calf body mass, and that winter body mass, but not the autumn carcass mass, increased with increasing proportion of fair (Table 7B, Figure 3B).

Finally, the highest ranked model combining the effects of maternal conditions and proportion poor habitat was similar to the two aforementioned (Table 6C). The alternative model with lowest $\Delta AICc$ also included the interaction between mothers age and proportion poor habitat, but with a $\Delta AICc$ of 1.51. Consequently, I chose the simpler model with highest rank as most likely among the combined maternal-poor habitat models. Also this model had similar maternal and habitat effects as the separate maternal model and poor habitat model. Hence, a negative relationship exists between the proportion poor habitat and winter body mass, but not between the proportion poor habitat and autumn body mass, and a positive association exists between mothers age and calf body mass (Table 7C, Figure 3C).

Table 6. AICc-based ranking of models explaining the variation in calf body mass in relation to mother's age and home range habitat composition. Full models are based on combinations of the highest ranked habitat and maternal effects models (Tables 2 and 4), and in some cases did not include the interaction between home range size and proportion habitat, or the interaction between proportion habitat and weight type (indicated with "-"). An X indicates that the variable was included in the model. Only the five highest ranked models for each habitat type and home range estimator are given (MCP = 95% minimum convex polygon, KDE = 95% kernal density estimator). Models are fitted as linear mixed models with year as random factor. An x indicates an interaction between two variables. Models with interactions always include the factor of both variables.

		HR size	Prop. habitat	Weight type	Mother age	HR size × prop. habitat	Prop. habitat × weight type	Prop. habitat × mother age	AIC _C value	ΔAIC _C	AIC _C weight		
A	Agriculture habitat and maternal effect	MCP	1	X	X	X	X	-	X	677.83	0.00	0.420	
			2	X	X	X	X	-		679.09	1.25	0.224	
			3	X	X	X	X	-	X	X	680.35	2.51	0.120
			4	X		X	X	-			680.89	3.06	0.091
			5	X	X	X	X	-		X	681.52	3.68	0.067
	1	X	X	X	X	-	X		672.93	0.00	0.588		
	2	X	X	X	X	-	X	X	675.35	2.42	0.176		
	3	X	X	X	X	-			676.05	3.14	0.122		
	4		X	X	X	-	X		678.17	5.24	0.043		
	5	X	X	X	X	-		X	678.50	5.57	0.036		
B	Fair habitat and maternal effect	MCP	1	X	X	X	X	-	X	671.41	0.00	0.609	
			2	X	X	X	X	-	X	X	673.78	2.36	0.187
			3	X	X	X	X	-			675.56	4.14	0.077
			4		X	X	X	-	X		676.27	4.85	0.054
			5		X	X	X	-	X	X	677.59	6.17	0.028
	1	X	X	X	X	X	X	X	673.06	0.00	0.340		
	2	X	X	X	X	X	X		673.93	0.87	0.220		
	3	X	X	X	X	X		X	675.12	2.06	0.121		
	4	X	X	X	X		X		675.74	2.68	0.089		
	5	X	X	X	X	X	X	X	675.85	2.79	0.084		
C	Poor habitat and maternal effect	MCP	1	X	X	X	X	-	X	668.16	0.00	0.603	
			2	X	X	X	X	-	X	X	669.67	1.51	0.284
			3		X	X	X	-	X		672.96	4.80	0.055
			4	X	X	X	X	-			674.32	6.15	0.028
			5		X	X	X	-	X	X	675.39	7.22	0.016
	1	X	X	X	X	X	-		670.59	0.00	0.447		
	2	X	X	X	X	X	-	X	671.86	1.28	0.236		
	3	X	X	X	X		-		672.22	1.63	0.198		
	4	X	X	X	X		-	X	673.66	3.08	0.096		
	5		X	X	X		-		677.24	6.66	0.016		

Table 7. Parameter estimates \pm SE, (95% confidence interval) from the highest ranked models explaining the variation in calf body mass by mother's age and proportion of different habitat types in her home range. MCP and KDE indicate whether mother's home range was estimated using 95% minimum convex polygon, or 95% kernel density estimator, respectively. Weight type is winter live body mass (intercept) or autumn carcass mass. 95% confidence interval was calculated based on 10,000 resamplings from the posterior distribution of the parameter estimates (for details, see Material and Methods, Statistical analyses).

		Intercept	HR size	Prop. habitat	Weight type	Mother age	HR size \times prop. habitat	Prop. habitat \times weight type	Prop. habitat \times mother age
A Agriculture habitat and maternal effect	M C P	185.19 \pm 4.56, (175.92; 194.48)	-0.59 \pm 0.21, (-0.01; -0.18)	73.74 \pm 26.92, (17.71; 124.88)	-104.41 \pm 6.17, (-116.16; -91.76)	1.54 \pm 0.53, (0.46; 2.56)	-	-74.40 \pm 40.35, (-150.77; 8.35)	-
	K D E	175.14 \pm 6.52, (162.72; 188.88)	-0.80 \pm 0.29, (-1.38; -0.21)	174.26 \pm 43.62, (81.64; 258.19)	-95.64 \pm 8.97, (-114.42; -78.89)	1.86 \pm 0.50, (0.76; 2.79)	-	-154.30 \pm 65.66, (-282.64; -24.33)	-
B Fair habitat and maternal effect	M C P	181.09 \pm 4.75, (172.14; 190.56)	-0.52 \pm 0.20, (-0.89; -0.11)	60.81 \pm 15.73, (28.57; 90.40)	-103.70 \pm 5.73, (-115.50; -92.60)	1.84 \pm 0.50, (0.88; 2.83)	-	-59.45 \pm 22.54, (-101.63; -10.78)	-
	K D E	173.62 \pm 13.34, (145.14; 199.38)	1.54 \pm 1.10, (-0.56; 3.82)	97.43 \pm 56.10, (-13.44; 212.70)	-103.78 \pm 6.75, (-118.25; -91.06)	-0.34 \pm 1.54, (-3.33; 2.73)	-10.85 \pm 4.53, (-19.75; -1.66)	-55.67 \pm 26.00, (-105.57; -1.87)	13.00 \pm 7.26, (-1.25; 27.60)
C Poor habitat and maternal effect	M C P	221.36 \pm 7.38, (206.39; 235.84)	-0.52 \pm 0.20, (-0.92; -0.15)	-58.81 \pm 13.69, (-84.88; -30.66)	-144.93 \pm 9.89, (-163.33; -123.29)	1.89 \pm 0.49, (0.92; 2.89)	-	61.13 \pm 20.50, (16.99; 100.36)	-
	K D E	253.75 \pm 20.40, (213.93; 295.28)	-4.43 \pm 1.86, (-8.11; -0.71)	-132.02 \pm 43.76, (-223.81; -50.97)	-117.97 \pm 2.59, (-123.16; -112.81)	2.51 \pm 0.54, (1.43; 3.57)	8.04 \pm 4.07, (-0.20; 15.96)	-	-

4. Discussion

Understanding the mechanisms that generate individual variation in life history traits is a key challenge in population ecology (Beckerman et al. 2006). In my study, I investigated how habitat qualities in home range are important for body mass in moose. Calf body mass has large impact on future individual fitness (Lindström 1999), such as age at maturity and survival. Accordingly, a better understanding of the mechanisms behind the individual variation in this life history trait is important for our general understanding of the moose population dynamics and for predicting the consequences of management actions and environmental changes on moose populations. I found that calf body mass depended on both maternal effects, and on habitat qualities within the summer home range of mothers (Figure 3). This supports the prediction that maternal effects operates through mothers age, and the prediction that availability of resources in the home range of mothers affects the body mass the calves are able to obtain during their first year of life. However, mother's choice of summer home range did not seem to generate significant differences in calf body mass by the end of summer (Figure 3), rather the effect was present first after including also the autumn and winter period for body growth of calves.

Maternal effects are often defined as non-genetic correlations between the calf's phenotype and the mother's phenotype and/or her environment (Mousseau and Fox 1998). One important correlate is mother's body mass and the body mass of her offspring. Unfortunately, I did not have mother's body mass for a satisfactory number of individuals to run reliable statistical tests, but exploratory tests indicated a positive relationship between mother's body mass and calf carcass or live body mass. This relationship disappeared when also including mother's age, suggesting that age is a good variable for maternal effects on calf body mass. Age of a mother can affect calf body mass through several mechanisms, in addition to the size-effect.

In birds, breeding experience has been shown to be a key trait for reproductive performance by affecting the timing of breeding and efficiency of foraging (e.g. Sydeman et al. 1991; Laaksonen et al. 2002; Nager and van Noordwijk 1995) and similar mechanism may also be relevant for moose. For instance, ovulation occur later in the autumn for 1.5 years old females than for older females (Garel et al. 2009), and late ovulation leads to late birth in the

following year (e.g. Sæther et al. 2003). This can lead to a shorter period for calf body growth until the hunting or marking season, which could be an explanation for the effect of mother's age on calf body mass. However, as the calf body mass was adjusted for birth date, this effect was already accounted for. An alternative explanation is that calves that are born early have access to food of higher quality (and for a longer period of time) compared to calves that are born late. In other words, a better match between the environmental phenology and birth date may be essential (Post and Forchhammer 2008). If this is accompanied by experienced mothers being better in utilizing the spatial variation in food resources during the summer period, calves will benefit from this indirectly through lactation, and directly through foraging in high-quality patches. However, a better utilization of foraging resources should be accompanied by habitat effects on calf body mass.

I found calf body mass to be related to the habitat composition of mother's home range, but only for body mass measured during winter. Winter body mass was positively related to proportion of agriculture areas and fair foraging ranges, and negatively related to the proportion of poor ranges in mothers summer ranges. This indicates a complex relationship between mother's choice of home range and her fitness-related traits.

I did not find any effect of habitat quality on autumn body mass of calves. This was not predicted, but can have several possible explanations. Firstly, the moose in Vega are in superb condition as their body size is among the largest and the population among the most productive in Norway (Solberg and Heim 2006; Sæther et al. 2007; Solberg et al. 2011). This suggests that they have access to high abundance of forage of high quality. Because conditions during summer has shown to be more important than winter conditions for moose body mass variation in Norway (Herfindal et al. 2006; Sæther et al. 1996), the high performance of moose at Vega suggests that summer foraging conditions are of high quality. Consequently, variation between individuals in foraging resources during summer may not be adequate to generate variation in calf body mass that could be detected in autumn body mass. Second, during parts of summer, particularly during the first month, calves are mainly consuming milk (e.g. Schwartz 1998) and not directly affected by variation in foraging conditions. This may have blurred the habitat effects on the calves' autumn body mass. By mid-winter, however, the calves have had a longer period of varying foraging conditions, which is reflected as an effect of habitat availability on their body mass.

During autumn, moose utilize agricultural areas extensively (Bjørneraas et al. 2011). These areas offer abundant fresh vegetation after the late harvest, and fresh vegetation is expected to be of higher quality than old and mature vegetation (Klein 1970), which can have large impact on body growth through the multiplier effect (White 1983). It is therefore not surprising that access to agricultural areas during autumn affect the body mass of calves a few months later. In addition, during snow-free periods of autumn and winter, bilberry bushes are important forage (Bergström and Hjeljord 1987). The habitat class "fair habitat" at Vega was recognized by high cover of bilberry (Angeloff et al. 2004; Herfindal et al. 2009). In contrast, the poor habitat class had higher abundance of bogs and wetlands, heather and lichen, which are not preferred by moose (Bergström and Hjeljord 1987). This can explain why fair habitat is associated with higher calf body mass, whereas calves with high proportion of poor habitats are of smaller size during winter.

I used the mother's summer home range as a measure of habitat availability for the analyses on both autumn and winter body mass. This assumes that areas used during autumn and winter overlaps highly with the summer home ranges. There were only few individuals with sufficient data during autumn and winter to calculate season-specific home ranges, which would have been preferable for the analyses of winter body mass of calves. However, moose females at Vega seem to show a relatively high fidelity to their summer ranges all year round (Morten Heim, pers. obs.), which is to be expected given the lack of large scale gradients in the landscape (Rolandsen et al. 2010). It is therefore reasonable to believe that the summer ranges constitute a good representation also of the autumn and winter ranges. Still, a better evaluation of the seasonal overlap in space use should be performed to better evaluate the role of home range and habitat selection on individual's fitness.

Interestingly, both the effect of mother's age and her summer habitat composition remained significant in the combined effects models. If, for instance, the habitat composition was a result of a better knowledge of available resources with age and experience, I would have expected that the effect of either age or habitat was reduced in the combined models. When this was not the case, it suggests that quality of the home range and age and experience is not linked in moose at Vega. The maternal effect is thus not simply caused by a better location of the home range on the island. It can, however, be that experienced females are better in utilizing the resources within their ranges. The distribution of forage resources in the

landscape will vary within and between seasons, and the ability to track such spatiotemporal environmental dynamics can be a trait that is age-dependent.

In the analyses of habitat composition of moose cows, it was important to use a representation of the individuals' actual habitat availability. Home range estimators are commonly used to draw inferences about individuals' habitat availability and use, but different estimators are associated with challenges. For instance, the minimum convex polygon (MCP) often overestimates the home range size and thereby also overestimate the available habitat (Börger et al. 2006a; Nilsen et al. 2008). The kernel-based estimators (e.g. KDE) imply setting several parameters a priori, and these parameters can have great influence on the size and shape of estimated home ranges. I used both MCP and KDE as estimators of the summer home range, and assessed to what extent the result depended on the choice of method.

My findings were that the overall conclusions did not depend on the choice of home range estimator (Table 6). There were some minor differences in the preferred models. For instance, for fair habitat, the best combined effects model differed between MCP and KDE. For KDE, the effect of proportion fair habitat depended on both home range size, and on mother's age, while these interactions were not included when using MCP (Table 6). The 95% confidence interval for the interaction between mother's age and proportion fair habitat included zero, suggesting a high uncertainty in this combined maternal and habitat effect. The negative estimate for the interaction between proportion fair habitat and home range size did not include zero (Table 3). Thus, for KDE it appears that the benefit of a high proportion of fair habitat is reduced for large home ranges. This can indicate that it is the absolute availability, rather than the relative availability of fair habitat, that is important. However, since the MCP did not suggest such results, and I did not find support for such relationship for other habitat types, I choose to focus on the simpler relationship.

In this study I documented that variation in calf body mass depend on both mother's age and habitat composition. Early conditions are often life lasting in mammals (Lindström 1999; Solberg et al. 2004; Solberg et al. 2008). My results therefore suggests that moose calves born from an experienced mother that inhabits a favourable home range gets a better start of life, thus expected to have a higher lifetime reproductive success. Such differences in early conditions are often referred to as the silver spoon effect (van de Pol et al. 2006). Although studies show fitness consequence of habitat utilisation (McLoughlin et al. 2007), few studies

have documented that such habitat effects on life history traits can occur already during the first year. Individual variation in fitness-related traits is now being recognised as a driver also for population dynamical processes (e.g. Vindenes et al. 2008). Many ungulate populations experience large changes in habitat quality caused by fragmentation, landscape degradation and climate change (Bolger et al. 2008). Therefore, it is important to know how such changes can generate long lasting variation in fitness, and in turn affect the population dynamics.

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