The Fat Advantage: Investigating the Link Between Fat Reserves and Reproductive Success in Female Moose

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The Fat Advantage - Investigating the Link Between Fat Reserves and Reproductive Success in Female Moose

Fördelen med fett – En undersökning av kopplingen mellan fettreserver och reproduktiv framgång hos älgkor

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Abstract

Understanding the relationship between body condition and reproductive success is essential for effective wildlife management. In this study, we investigated whether fat reserves influence fecundity in female moose (*Alces alces*) in Sweden. Using data from harvested individuals, we assessed fat content from bone marrow and slaughter weight as indicators of body condition and counted corpora lutea (CL) as a proxy for reproductive potential. A Poisson regression revealed a positive association between fat content and fecundity, with slaughter weight also contributing significantly. However, when individuals were grouped by fecundity (0, 1, or ≥2 CL), ANOVA and Tukey HSD post-hoc tests showed no significant differences in fat content between groups. In contrast, CL-2 individuals were significantly heavier than those in lower fecundity groups, suggesting that body mass may be a more reliable predictor of reproductive output. A second ANOVA showed no significant age differences among fecundity groups, indicating that age was not a confounding factor. These findings suggest that while fat reserves may play a role in reproductive success, body weight is a stronger indicator, and age does not significantly influence fecundity in this population.

Keywords: Alces alces, moose, Sweden, life history, body condition, reproduction

Sammanfattning

För att effektivt kunna förvalta viltpopulationer är det viktigt att förstå sambandet mellan kroppskondition och reproduktiv framgång. I denna studie undersökte vi om fettreserver påverkar fertiliteten hos älgkor (*Alces alces*) i Sverige. Med hjälp av data från fällda individer analyserade vi fettinnehåll i benmärg och slaktvikt som indikatorer på kroppskondition, samt antalet gulkroppar (corpora lutea, CL) som mått på reproduktionspotential. Ett positivt samband mellan fettinnehåll och fertilitet visades med hjälp av en Poisson-regressionsmodell, där även slaktvikten visade sig ha en signifikant effekt. Däremot, när individerna delades in i fertilitetsgrupper (CL-0, CL-1, CL-2), visade både ANOVA och efterföljande Tukey HSD-test inga statistiskt signifikanta skillnader i fettinnehåll mellan grupperna. Däremot var CL-2-individer signifikant tyngre än de med lägre fertilitet, vilket tyder på att kroppsvikt kan vara en mer tillförlitlig indikator på reproduktiv förmåga. En uppföljande ANOVA visade inga signifikanta åldersskillnader mellan grupperna, vilket innebär att ålder inte var en förväxlingsfaktor. Resultaten tyder på att även om fettreserver kan spela en roll för reproduktiv framgång, är kroppsvikt en starkare indikator, och ålder påverkar inte fertiliteten i denna population.

Nyckelord: Alces alces, älg, Sverige, livshistoria, kroppskondition, reproduktion.

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1. Introduction

1.1 Background

Moose (*Alces alces*) are one of the largest deer species and a key part of Fennoscandian forest ecosystems. They browse vegetation and can shape forest communities, making them important indicators of habitat health (Crichton 1998). In Sweden there is a very high density of moose compared to other countries (Lavsund et al. 2003), partly because modern forestry interventions create many clear-cuts, which are food-rich stands for moose. The number of moose was estimated to be around 200,000 at the end of the 2024 hunting season (Widemo & Leonardsson 2024). High moose densities bring both benefits and challenges; moose have ecosystem services, such as recreational hunting and tourism. However, very high densities on the other hand can lead to damages on trees caused by browsing which may result to economic losses for forest owners (Lavsund et al. 2003).

Understanding the factors that influence moose populations is essential for effective management. Different factors, such as the food quality, population density, and predation risk, influence physiological attributes like body mass and fat reserves (Heard et al. 1997). Furthermore climate change and thus, warmer weather in Scandinavia has already been linked to lighter moose calves and lower survival (Holmes et al. *2023*). Physiological changes can affect the fertility in the species (Heard et al. 1997). Sand (1996) found that there were positive relationships between age, body size, and fecundity, particularly in terms of ovulation rates. Understanding these reproductive dynamics and the biological and ecological factors that influence reproduction in moose is essential. Thus, wildlife management should aim at monitoring moose health and reproduction.

Female moose build up fat reserves in summer, when food resources are abundant, to reproduce, care for their offspring, and survive winter. Female moose without enough fat may fail to maintain pregnancy or give birth to fewer or weaker calves. In harsh more seasonal climates, like Scandinavia, greater body mass is necessary to maintain reproductive success compared to milder and less seasonal climatic conditions (Sand 1996). If winter browsing is limited, female moose and calves can have high mortality rates (Ausilio et al. 2024). Consistent with that, research in

Sweden has shown that heavier female moose have higher rates of ovulation. Consistently, yearling moose are more likely to ovulate once their carcass weight exceeds approximately 150 kilograms. Measurements of fat reserves and body weight are an important tool for assessment of the condition of *Cervidae*, enabling evaluation of the animals' environmental living conditions (Czyżowski et al. 2021). Biologists therefore use measures like carcass weight or bone marrow fat from harvested moose as indicators of condition, low bone marrow fat, for instance, is a reliable sign of poor nutrition (Hundertmark & Schwartz 1993). Given this link between nutrition and reproduction we focus on two measurements, the number of corpora lutea, as a measurement of reproduction rate and bone marrow fat from sampled adult female moose.

1.2 Moose reproduction

Breeding

Moose, like many other large mammals, exhibit substantial variation in reproductive patterns across species, populations, and individuals (Sand 1996). Moose is a seasonally polyestrous mammal, with mating typically occurring in a short time period during autumn (Miquelle 1990). The oestrous period for female moose generally spans from late September to early October. The breeding period is highly synchronized across the distribution of the species (Schwartz 1992). Due to a gestation of about 7–8 months, calves are born in late spring or early summer when forage is most abundant (Schwartz 1992). Exact rut dates can shift depending on latitude and annual weather but mainly similar among regions.

The Fennoscandian moose populations tend to be skewed towards younger females due to annual hunting (Malmsten et al. 2014). Consequently, age and weight at puberty are critical for population dynamics, as they determine the proportion of pregnant females.

While hunting can alter population demographics, it is the selectivity of harvest where, for example, removing large adult bulls or older female moose shapes the age and sex structure. Such selective harvesting can skew a population towards younger female animals(Malmsten et al. 2014).

Puberty, sexual maturity and reproductive physiology

Malmsten et al. (2014) defines puberty as the age at which the first ovulation occurs following oestrus, whereas sexual maturity is the age when the animal produces its first offspring. In moose, the number of ova produced each breeding season is tied to the cow's age and nutritional status (Solberg et al. 2002). Typically, one or two (rarely three) dominant follicles mature in the ovary and older female moose in good body condition tend to ovulate more follicles per oestrus (Malmsten et al. 2014). When the female enters heat, ovulation occurs, and the eggs will be released. Female moose, with good body condition can potentially produce more embryos. Furthermore, older females with a better body condition tend to ovulate more frequently. The follicular cavity then develops into one or more corpora lutea. If mating does not occur and the breeding season continues, the corpora lutea breaks down (luteal regression), and the cycle begins again.

There are anatomical differences between the uterus of a heifer (nulliparous female) and a cow (multiparous female). A heifer's uterus is more slender and smoother whereas a cow's uterus exhibits thicker walls, more prominent blood vessels, and fibrous folds, changes resulting from previous pregnancies (Sæther & Haagenrud 1983).
There is still uncertainty about whether ovulation in moose takes place during standing oestrus or immediately afterward. In southern Sweden, it is generally observed that the first ovulation of the season occurs before the hunting season begins, based on mating dates and the presence of developed corpora lutea. According to Schwartz (1992) pregnancy can range from 216 to 240 days with a mean of 231 days.

Body condition and fecundity
Body condition in terms of fat reserves strongly influences pregnancy success and calf production in moose (Ruprecht et al. 2016). For example, studies using rump fat as a body condition index show that female moose with at least 2 mm of rump fat had a pregnancy rate of 95% (Ruprecht et al. 2016). Likewise, the chance that a pregnant cow produces at least one calf rises roughly in proportion to maternal fat with no sharp threshold found (Ruprecht et al. 2016). In other words, female moose with greater fat reserves not only conceive more often but are also more likely to successfully carry a pregnancy to term.

Maternal age interacts with nutrition in shaping fecundity. Females that grow quickly and reach sufficient body weight by puberty can become pregnant at a younger age, increasing their lifetime calf production (Malmsten et al. 2014). In contrast, poor nutrition delays usually the first conception of a female. In general, very young or very old female moose have lower pregnancy rates. Moose in their prime-age (3.5–8.5 years old), were in about 92% of the cases pregnant, whereas female moose younger than 3 or older than 9 years in average only around 32–38% (Ruprecht et al. 2016). Thus, age and body condition are primary determinants of reproductive output in female moose (Malmsten et al. 2014).

1.3 Nutritional status and fat reserves

Because body size and fat reserves have a direct influence on the timing and success of reproduction (Malmsten et al. 2014), examining fat reserves as a physiological indicator of nutritional condition and reproductive capacity is essential. According to Stephenson et al. (1998), nutritional status in moose can be estimated via lipid reserves. Lipids are the body's primary energy storage and are stored mainly in the form of triglycerides. In addition, estimating total body fat provides insight into reproductive and survival capability, energy balance and the habitat’s ability to support the nutritional needs. Stephenson et al. (1998) also notes that although proteins and carbohydrates contribute to energy metabolism, lipids provide more than double the energy per unit mass. Moreover, fat stores are depleted more rapidly than muscle tissue during times of scarcity. A common metric for assessing body condition in ungulates is the fat content of marrow from skeletal bones (Sand et al. 2012). These fat reserves are among the last to be metabolized during starvation. Marrow fat levels below 10%–30% indicate poor condition and increased risk of winter mortality.

Okarma (1989) found that red deer (*Cervus elaphus*) had lower mandible marrow fat than in long bones, although a positive correlation was still observed, especially in adult females (hinds). Therefore, mandible fat could serve as a reliable indicator of nutritional condition. Similarly, Spears et al. (2003) examined the relationships between marrow fat values in the long bones of moose and found a strong correlation between marrow fat content in various long bones and femur fat in both calves and adult moose. Fat loss occurred first in proximal and distal bones with distal bones being the last to be depleted. Davis et al. (1987) had similar results for caribou *(Rangifer tarandus granti*). Having established how marrow fat relates to body condition we now explore other factors related to body condition.

In order to achieve sustainable moose populations, it is important to understand key factors such as body condition and reproductive success. Although this relationship has been studied both in Sweden and internationally, certain knowledge gaps remain. The ongoing effects of climate change and rising global temperatures have heightened concerns about the future of moose populations (Holmes et al. 2021). Therefore, it is crucial to deepen our understanding of the relationship between fat reserves and fecundity.

1.4 The aim of the study

Given the importance of body condition in shaping reproductive outcomes, this study was designed to empirically test the link between fat reserves and fecundity in female Swedish moose. As measures of body condition, we are using slaughter weight and the fat content from the metacarpal bone marrow. The primary focus was to address the following research question; Is there a relationship between fat reserves and fecundity in female moose? We hypothesize that there is a significant relationship between fat reserves and fecundity in Swedish moose, with moose having higher fat reserves exhibiting better reproductive success.

2. Material and method

2.1 Lab procedure

Data on fat content from bone marrow samples was taken from the mandible (underjaw) and the metacarpal bone, as well as corpora lutea counts, slaughter weight, and age determined from tooth cementum annuli. All biological samples were obtained from hunters, who froze the samples in the field and shipped them on ice to SLU for analysis. Our sample data was primarily collected in the Västerbotten region, but also includes a wide geographical distribution across the following locations:

- Storuman
- Fredrika
- Lillhärdal
- Särna Västra
- Västra Idre
- Björna
- Stöttingsfjället
- Mickelkölen
- Myssjö-Oviken
- Hamra Noppikosk (Orsa)
- Ljusdal-Ramsjö
- Färila-Kårböle
- Ljusdal
- Umeälven
- Älghults
- Norramåla Ekhorva
- Skirö
- Särna Idre

2.1.1 Uterus samples

Upon arrival, reproductive tracts were thawed, and the ovaries were detached from the ovarian ligament for inspection; any follicular activity was recorded as present or absent, and the diameter of the largest follicle was measured. When corpora lutea were present, they were counted, their diameters recorded, and the degree of protrusion noted, after which the ovaries were fixed in 4 % formaldehyde. If the ovaries contained a large follicle (diameter > 10 mm), or one or more corpora lutea were present (indicating that ovulation had occurred) but no pregnancy was observed, oestrus was assumed to have taken place less than two weeks previously. The uterine horns were then opened to confirm the presence or absence of an embryo or fetus. Based on uterine vascularization and other morphological characteristics, each female was classified as either a cow (parous) or a heifer (nulliparous) and assigned to one of three reproductive states: between oestrus and implantation, pregnant, or unclassifiable. All measurements were performed with digital callipers to the nearest 0.1 mm, and observations were recorded on standardized datasheets.

Figure 1. Moose uterus (cut open) with enlarged blood vessels in the surface between the uterine wall and the broad uterine ligament, all sign of a previous pregnancy. Photo: Hanna Isaksson.

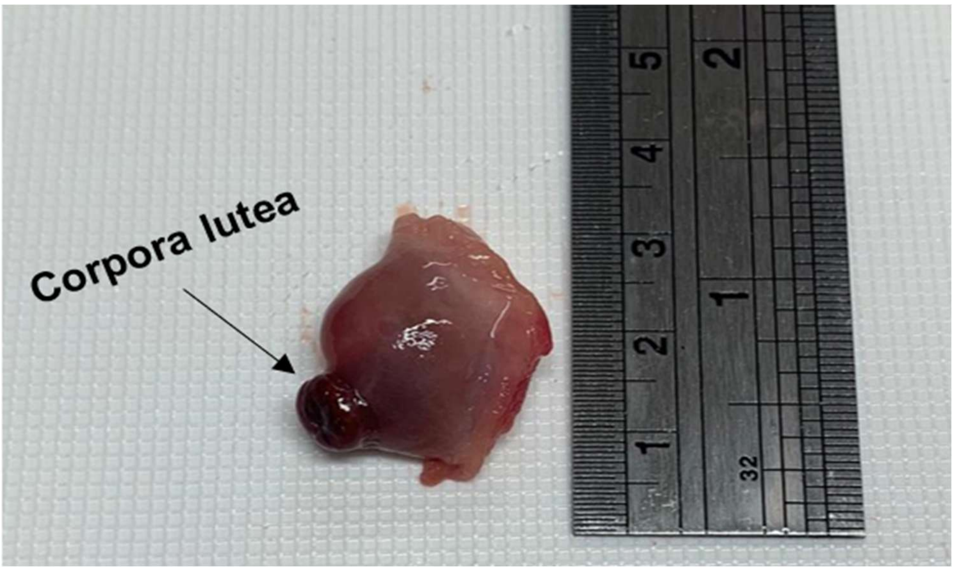

Figure 2. Female moose ovary with one corpora lutea. Photo: Hanna Isaksson.

2.1.2 Metacarpal samples

The metacarpal bone was measured and 20–30 grams of bone marrow was extracted from each sample. The sample was weighed (wet weight) and then dried in a drying cabinet, at 70 degrees, for approx. 2 weeks until no more weight loss was notable, before weighed again to determine weight loss. Based on both weights (wet weight and dry weight) the fat content percentage can be calculated.

Figure 3. Front leg opened from the back up to the dew claws and skinned on all sides to access the metacarpal bone. Photo: Carolin Berndt.

2.1.3 Mandible jaw

To determine age in moose, tooth cementum annuli were counted from cross-sections of the first permanent molar (M1). The M1 was cut in between the two cusps and angled to intersect the "vault" between the root attachments. The surfaces were smoothened with fine sandpaper to enhance visibility of cementum layers, and a few drops of oil were applied to increase contrast. Tooth sections were examined under magnification (8–15×), using a stereomicroscope.
Age was estimated by counting the lighter, wider summer zones in the cementum. As the first summer zone (from the calf stage) is typically absent, one year was added to the total ring count.

2.2 Statistics

All statistical analyses were performed using R (version 4.4.1) with a significance level set at $p < 0.05$. To analyze the count data, a Poisson regression model was applied to estimate the number of corpora lutea as a function of fat content (%) and slaughter weight (kg). The model's accuracy was assessed by comparing its predicted values with the observed counts. To further examine differences in fat content, slaughter weight, and age across fecundity groups (categorized as 0 CL, 1 CL, and 2 CL), separate one-way ANOVAs were performed for each variable. Post-hoc comparisons between fecundity groups were conducted using Tukey's Honest Significant Difference (HSD) test to identify significant pairwise differences. To verify assumptions for the ANOVA, residuals were visually inspected using Normal Q-Q plots and tested for normality with the Shapiro-Wilk test, confirming that residuals were approximately normally distributed. To investigate whether age differed significantly among fecundity groups, we conducted another ANOVA with age as the dependent variable and fecundity group as the independent factor. This analysis aimed to determine whether age could be a confounding factor in the observed differences in reproductive output. Prior to running the ANOVA, we assessed the assumption of normality using both a QQ plot and the Shapiro-Wilk test. The results indicated that the data were approximately normally distributed, with only minor deviations that did not violate the assumptions of the test.

2.2.1 Poisson regression assumptions

The Poisson regression model was based on the following assumptions:

i. The dependent variable is count data, which is satisfied since the number of corpora lutea is a non-negative integer count.

ii. The independent variables, fat content (%) and slaughter weight (kg), are continuous.
iii. Observations are independent, each moose was sampled individually without repeated measures.
iv. The count data are assumed to follow a Poisson distribution.
v. The mean and variance of the response variable (number of corpora lutea) are assumed to be equal (equidispersion).

Although overdispersion was not formally tested, model diagnostics and residual plots indicated an acceptable fit. These assumptions support the suitability of the Poisson regression model for our analysis.

3. Results

A sample size of 58 female moose were used in this study. Each individual was evaluated for body condition using slaughter weight and bone marrow fat content, while reproductive potential was assessed by counting the number of corpora lutea (CL) (Figures 4-9). Individuals were categorized into three fecundity groups: 0 CL, 1 CL, and 2 CL. The Poisson regression analysis revealed a significant positive relationship between slaughter weight and the number of corpora lutea (Figure 4, Figure 1), indicating that heavier individuals tended to have higher reproductive potential. In contrast, fat content did not show a statistically significant effect on fecundity. Further analysis using ANOVA and Tukey HSD post-hoc tests confirmed that there were no significant differences in fat content between the fecundity groups (Figure 5, Table 2). However, slaughter weight differed significantly, with individuals in the 2 CL group being significantly heavier than those in the 0 CL and 1 CL groups (Figure 6,Table 3). Age did not differ significantly between fecundity groups (Figure 7, Table 4. ANOVA results testing for differences in age across fecundity groups.Table 4), suggesting that age is unlikely to have influenced the observed relationships. These findings suggest that body mass is a more reliable predictor of reproductive success than localized fat reserves, and that age does not significantly influence fecundity in this population.

3.1 Relationship between fat reserves and fecundity

The predicted corpora lutea (CL) count showed a slight increase with rising fat content, reaching a peak of around 90%, followed by a slight decline (Figure 4Figure 2). When individuals were grouped by slaughter weight category (low, medium, and high), no consistent trend was observed that would indicate a strong influence of weight category on this relationship (Figure 4). Individuals across all weight categories were distributed fairly evenly across the fat content range, suggesting that slaughter weight did not systematically affect the association between fat content and CL count. However, the results revealed that slaughter weight had a statistically significant positive effect on the number of corpora lutea, with an estimated coefficient of 0.024 and a p-value of 0.0003, indicating significance at the 0.05 level (Table 1). In contrast, fat content did not have a significant effect on the number of corpora lutea, as reflected by a p-value of 0.803, which is above the significance threshold (Table 1).

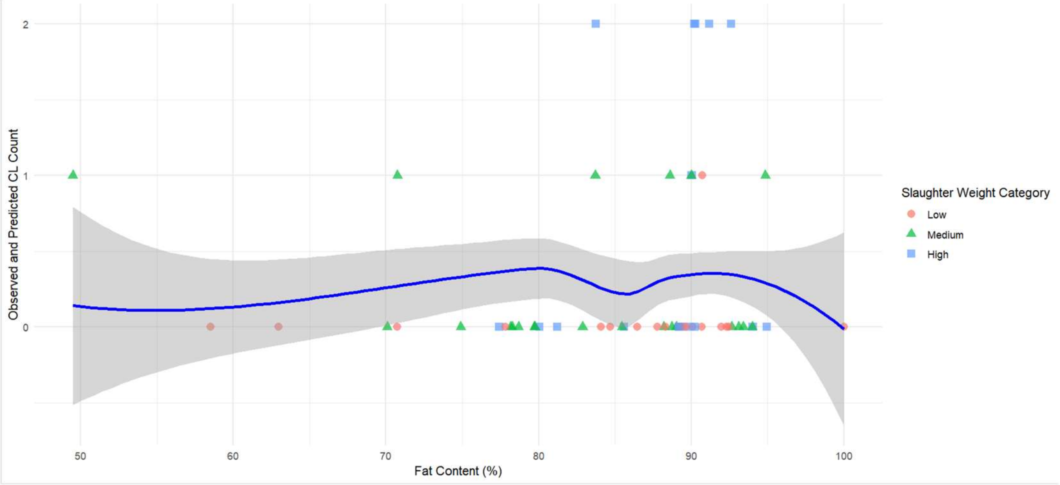

Figure 4. Predicted corpora lutea (CL) count in relation to fat content (%) and slaughter weight in female moose, based on a Poisson regression model. The blue line represents the model's predicted CL count across fat content levels. Data points are categorized by slaughter weight: low (red circles), medium (green triangles), and high (blue squares). Weight categories were defined using quantiles: low (≤144.48 kg), medium (144.49–199.58 kg), and high (>199.58 kg).

Table 1. Poisson regression results for fat content and slaughter weight as predictors of the number of corpora lutea in female moose.

Predictor	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
(Intercept)	-4.94	2.91	-1.70	0.089
Fat content	-0.009	0.035	-0.25	0.803
Slaughter weight (kg)	0.024	0.0066	3.59	0.0003

The distribution of fat content across the fecundity groups revealed that the median fat levels were similar, approximately 90% (Figure 5). However, there were some differences in fat content among the groups. The group with two corpora lutea showed the least variability in fat content, the groups with zero and one CL showed more variation, including a few individuals with notably lower fat percentages (Figure 5). The analysis also revealed no statistically significant differences in fat content among the different fecundity groups (Table 2). All pairwise comparisons yielded adjusted p-values greater than 0.05; CL-0 and CL-1 (p = 0.691), CL-0 and CL-2 (p = 0.584), and CL-1 and CL-2 (p = 0.361), and did not show meaningful differences (Table 2). Furthermore, the 95% confidence intervals for each of these comparisons included zero, providing additional evidence that fat content does not significantly differ between the fecundity groups examined (Table 2).

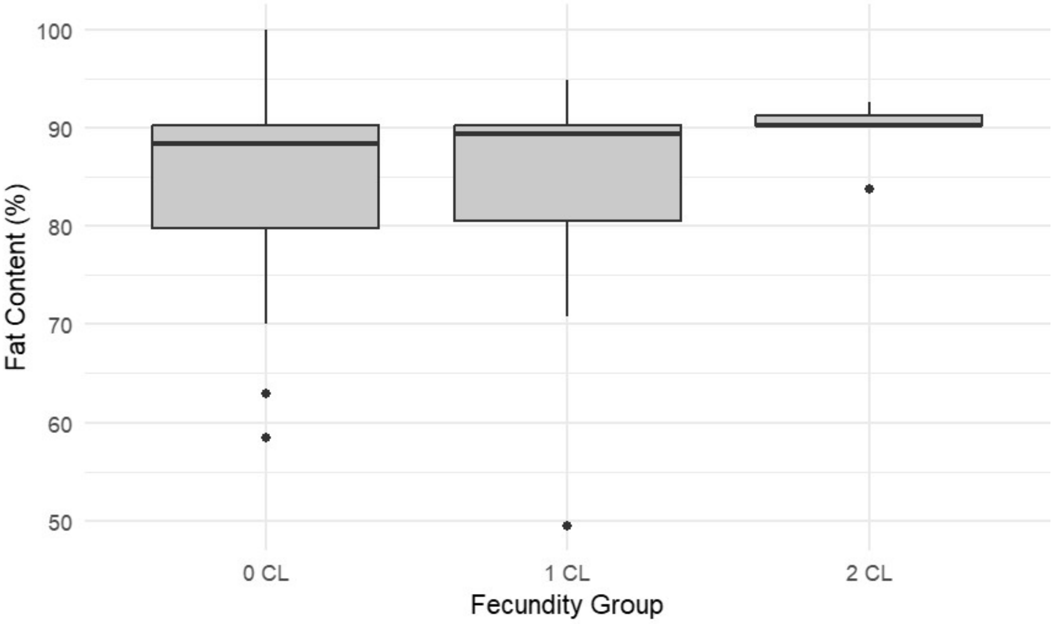

Figure 5. The distribution of fat content (%) across fecundity groups.

*Table 2. Tukey HSD post-hoc comparisons of fat content between fecundity groups (CL-0, CL-1, CL-2)**,** adjusted p > 0.05.*

Comparison	Difference (diff)	95% CI (lower to upper)	Adjusted p-value
CL-0 vs CL-1	–2.95	–11.61 to 5.70	0.691
CL-0 vs CL-2	+4.38	–6.25 to 15.01	0.584
CL-1 vs CL-2	+7.34	–5.52 to 20.19	0.361

3.2 Relationship between slaughter weight and fecundity

The analysis demonstrated clear differences in slaughter weight among the three fecundity groups. The results indicate that individuals in 2 CL group had the highest median slaughter weight, exceeding 200 kg, following by those from 1 CL and 0 CL. 0 CL group displayed the widest range of weights, with several individuals weighing under 100 kg, while 2

CL group had the most consistent weights (Figure 6). The mean slaughter weight was 79.41 kg higher in the 2 CL group compared to the 0 CL group (p = 0.001), and 64.34 kg higher compared to the 1 CL group (p = 0.036) (Table 3). Both of these differences were statistically significant, as their 95% confidence intervals did not include zero. In contrast, the difference in slaughter weight between the 0 CL and 1 CL groups was not significant (p = 0.651), with a confidence interval that included zero (Table 3).

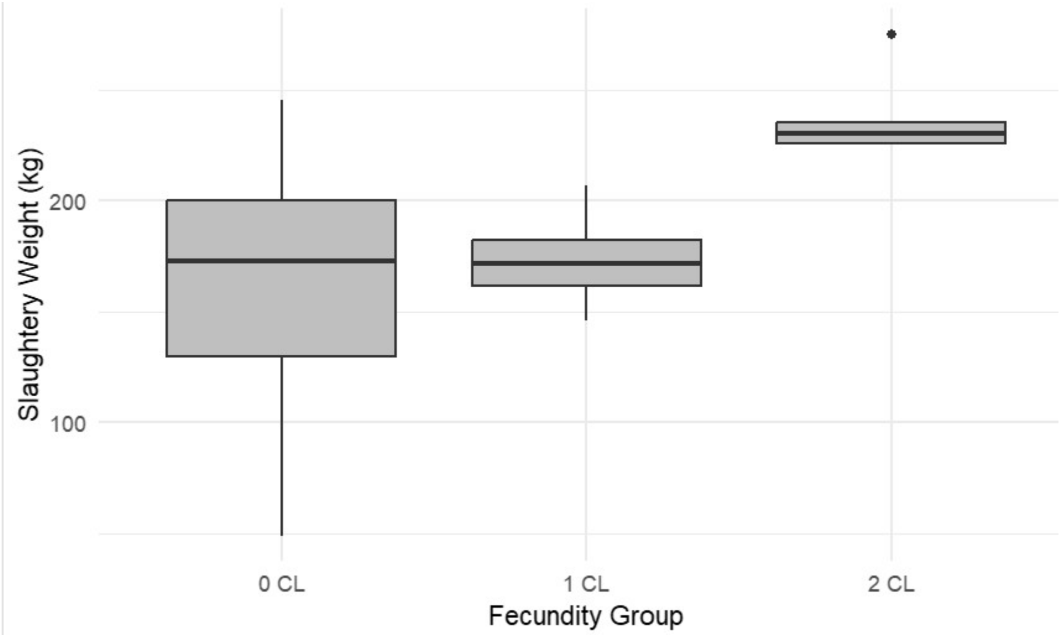

Figure 6. Slaughter weight (kg) across fecundity groups.

Tukey HSD post-hoc test:

Table 3. Tukey HSD post-hoc comparisons of slaughter weight between fecundity groups (CL-0, CL-1, CL-2).

Comparison	**Difference (diff)**	**95% CI (lower to upper)**	**Adjusted p-value**
CL-0 vs CL-1	+15.07	–25.90 to 56.04	0.651
CL-2 vs CL-0	+79.41	+29.07 to 129.74	0.001
CL-2 vs CL-1	+64.34	+3.47 to 125.21	0.036

3.3 Relationship between age distribution and fecundity

The age distribution across fecundity groups showed similar median ages among all groups (Figure 7). However, the 0 CL group exhibited the widest range of ages, while the 1 CL and 2 CL groups had a narrower age distribution, with most individuals clustered around the mid-range ages (Figure 7). No extreme values were observed across the groups. The mean square for fecundity group was 1.07, while the residual mean square was 33.60, indicating that the variation within groups was much larger than the variation between them (Table 4). The F-value was 0.032, and the p-value was 0.969, showing no meaningful differences in age between the groups (Table 4).

When comparing the results for age distribution and slaughter weight in relation to fecundity, distinct differences were observed between the fecundity groups (Figure 8). The 0 CL group displayed the greatest variability in both age and slaughter weight, comprising both younger and older individuals, as well as lighter and heavier ones. In contrast, the 1 CL group showed less variation, indicating a more consistent distribution, with individuals generally falling within a similar age and weight range (Figure 8). Finally, the 2 CL group exhibited the least variation, with individuals tending to be older and heavier than those in the other groups (Figure 8).

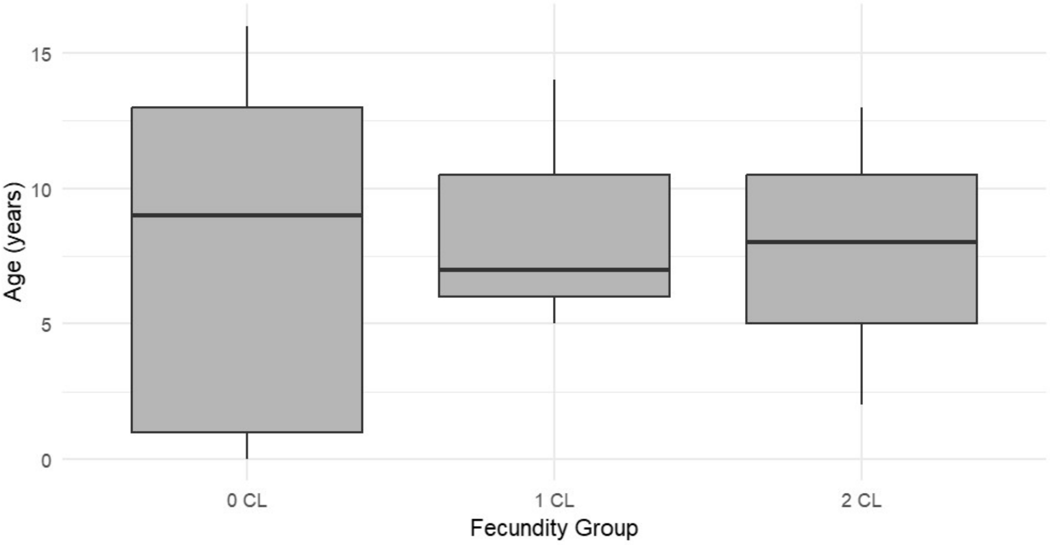

Figure 7. Age distribution (years) across fecundity groups.

Table 4. ANOVA results testing for differences in age across fecundity groups.

Source	**Df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Fecundity Group	2	2.1	1.07	0.032	0.969
Residuals	16	537.6	33.60		

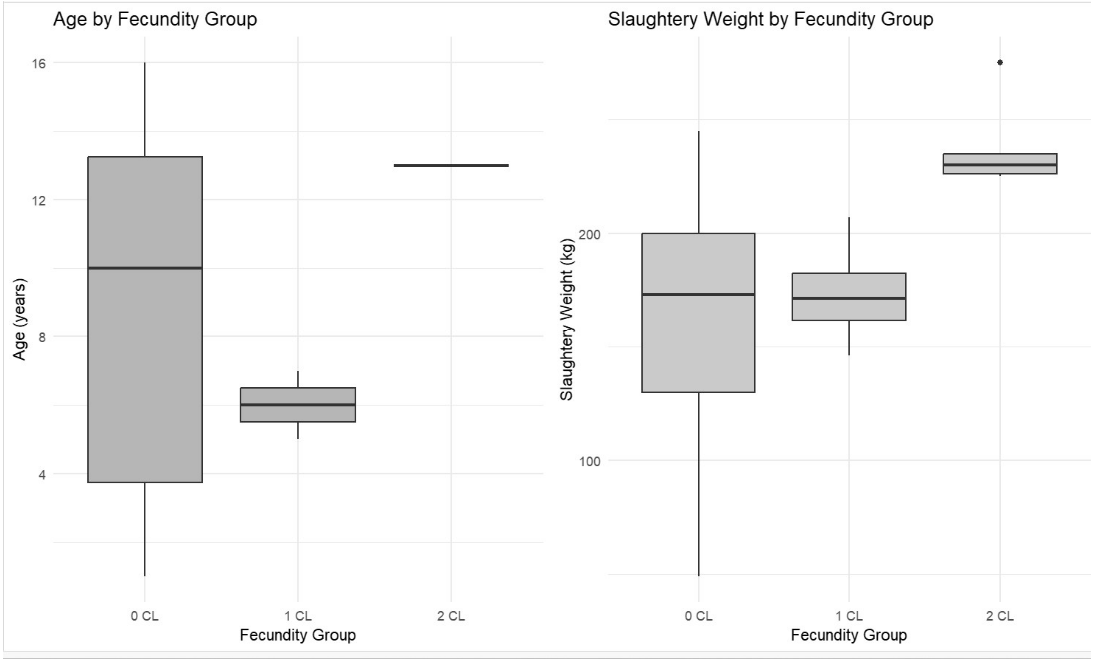

Figure 8. Comparing age (years) (left) and slaughter weight (kg) (right) across fecundity groups.

4. Discussion and Conclusions

This study aimed to investigate whether fat reserves, measured by slaughter weight and bone marrow fat content, are associated with fecundity in Swedish female moose. By analyzing these indicators of body condition alongside the number of corpora lutea, we tested the hypothesis that moose with higher fat reserves exhibit better reproductive success, potentially due to better body condition or other related traits.

The ANOVA analysis revealed no significant differences in bone marrow fat content between fecundity groups (Figure 5) suggesting that fat storage might be independent of reproductive status within this northern Swedish range population. However, slaughter weight showed a positive relationship with fecundity (Figure 6): for every 1 kg increase in weight, the expected number of corpora lutea increased by approximately 2.4% (Table 1. Poisson regression results for fat content and slaughter weight as predictors of the number of corpora lutea in female moose.Table 1),. This pattern may suggest that there might be a selection bias where heavier or animals, which are in a better condition, may be more likely to have multiple offspring or that females with two CL might be older and thus naturally heavier. Contrastingly, age did not differ significantly among fecundity groups (Figure 7), indicating that it is unlikely to be a confounding factor. This supports our assumption that differences in reproductive potential are more closely linked to body condition than to age-related effects.

Beyond body condition and age, additional factors could influence fecundity in moose. Social hierarchy among females may mediate access to critical resources, with subordinate individuals exhibiting lower fecundity. Variation in forage quality and habitat heterogeneity also plays a pivotal role; differences in browse species composition and plant phenology can constrain nutrient intake and ovarian function (Pettorelli et al. 2005) Parasitism and disease, including infections such as winter ticks or pathogens associated with chronic wasting disease, can impair nutrient absorption and redirect energy from reproductive processes to immune responses, thereby reducing fecundity in moose populations (Murray et al. 2006). Genetic variation in reproductive strategies or metabolic efficiency may likewise underlie individual differences in fecundity independent of measured body condition (Hewison & Gaillard 2001). Furthermore, climatic and photoperiodic factors such as winter severity, snow depth, and the timing of spring can affect the onset of oestrus, with harsher winters or delayed springs suppressing reproductive cycling (Parker et al.

2009). Finally, predation risk and the associated behavioural stress can shift energy allocation away from reproduction toward vigilance and escape behaviours, further diminishing fecundity (Creel & Christianson 2008).

Our finding that overall body mass seems to be a better explanatory variable than marrow fat for reproductive output aligns with Sand (1996), who reported stronger correlations between carcass weight and ovulation rates than between more localized fat indices and fecundity. Similarly, Sæther & Haagenrud (1985) found that moose carcass weight thresholds (≈150 kg) determined first ovulation in yearlings, suggesting that a certain mass may be required to support reproductive physiology. In contrast, Ruprecht et al. (2016) documented a near-linear increase in pregnancy probability with rump fat thickness but did not simultaneously assess body mass. Our results suggest that, at least in this population, mass may integrate the cumulative effects of both fat and lean tissues more robustly than bone marrow fat alone.

Two, non-exclusive mechanisms may explain why body mass better predicts fecundity than marrow fat content per se. First, slaughter weight captures total energy reserves, including both lipid and protein stores, which together has effects on follicular activity (Stephenson et al. 1998). Second, heavier females may reflect superior foraging success or home range quality and those factors are known to enhance both condition and reproductive investment (Heard et al. 1997). More generally, larger body size itself may confer reproductive advantages, as bigger moose may have inherently higher fecundity than smaller individuals, independent of short-term condition(Sand 1996). Marrow fat has been suggested as a potential indicator of short-term nutritional stress, with its levels possibly changing with the seasons and being affected by the order in which fat is drawn from various bones in the body (Hundertmark & Schwartz 1993; Spears et al. 2003), thereby obscuring longer-term condition signals relevant to reproduction.

However, our sample size was limited (n = 58), which reduces the statistical power of the analysis. All of this should be considered when interpreting the results.

From a wildlife management perspective, carcass weight may serve as a practical field index for monitoring reproductive potential in harvested moose. Given the stronger weight–fecundity linkage, managers could set weight-based harvest guidelines to maintain optimal reproductive output. Conversely, relying only on marrow fat analyses may misrepresent reproductive capacity, leading potentially to suboptimal management decisions.

To build on these results, future studies should increase the sample size across multiple seasons and regions to verify generality. Integrating various condition metrics such as ultrasonographic measurements of rump fat, serum metabolite levels, and assessments of both fat and lean tissue can help clarify the individual contributions of these factors. To further support management decisions, we recommend longitudinal monitoring of individual females to link pre-rut condition not only to calf survival, but also to broader measures of reproductive performance, including fertility and lifetime reproductive success, rather than focusing solely on fecundity. As well as assessing habitat and forage quality to connect environmental variation with condition and reproduction.

To conclude, our results indicate that, in this Swedish moose population, overall body mass is a more reliable predictor of ovulation rate, and therefore fecundity, than localized bone marrow fat reserves. Age did not confound these relationships, suggesting body mass integrates critical energy reserves and ecological advantages necessary for reproduction. Incorporating carcass weight into population monitoring protocols could therefore enhance the effectiveness of moose management and conservation strategies.

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Appendix

Appendix A: Glossary of key biological and reproductive terms used in the study.

Table 5. Definitions of key biological and reproductive terms used in the study.

Term	**Definition**
Polyestrous	Having multiple estrous (reproductive) cycles within a year.
Oestrus	A recurring period of sexual receptivity and fertility in female mammals, commonly referred to as "heat."
Corpora lutea (CL)	Hormone-producing structures in the ovary formed after ovulation
Polygynous cervids	Species within the deer family (Cervidae) in which one male mates with multiple females.
Nulliparous	A female that has never given birth.
Parous	A female that has given birth at least once.
Cementum annuli	Growth layers in teeth used to estimate age in mammals
Fecundity	Reproductive capacity
Fertility	Reproductive success

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