Influence of female reproductive status on mating behaviour in reindeer (*Rangifer tarandus*)

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Abstract

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Sexual selection drives reproductive strategies, particularly in highly polygynous species. In ungulates, a common strategy for securing exclusive access to females during the mating season is the formation of mating groups, consisting of a dominant male, multiple females and a few subordinate males. Defending these groups from rivals while courting females is energetically costly for males, whereas females are choosy and prefer high-quality males. To optimize mating investment, both sexes are expected to adjust their behaviour based on female reproductive status. This study examines how female reproductive status (fertilized vs. unfertilized) influences the mating behaviour of reindeer (*Rangifer tarandus*). For this purpose, a field experiment was conducted on semi-domesticated reindeer in Finland. We found that males courted unfertilized females significantly more frequently than fertilized ones, whereas female activity budgets did not differ with reproductive status, likely due to activity synchrony within mating groups. Moreover, the proportion of unfertilized females was significantly higher in the core areas of mating groups compared to both mating groups overall and the entire population. Male rank also affected these patterns, with the highest-ranking male courting and remaining close to a higher proportion of unfertilized females than lower-rank males. These findings demonstrate that beyond direct competition, males in polygynous systems exhibit selective courtship behaviours, potentially to increase reproductive success while reducing the cost. Our study highlights the use of spatial strategies by females within mating groups that could help maximize reproductive opportunities with high-ranking males.

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Contribution of Authors

As the first author, I was responsible for the conception, data analysis and writing of the thesis. The study was originally conceived by Dr. Robert B. Weladji and Dr. Øystein Holand. Dr. Weladji also assisted with the statistical analysis, provided guidance throughout the research, and reviewed and corrected the thesis, while Dr. Holand collected the data and offered valuable feedback. Dr. Knut Røed was responsible for conducting paternity analyses.

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1. Introduction

Sexual selection, a pivotal force of evolution, refers to the differential reproductive success that results from competition for mates and access to fertilization (Safran et al., 2013). Traditionally, it has been conceptualized through two primary mechanisms: intrasexual selection, the competition for mates within sex, and intersexual selection, the selection of mates by one sex (Darwin, 1871). This framework has since been expanded to include additional processes such as coercion, sperm competition and cryptic female choice (Andersson, 1994; Andersson & Iwasa, 1996; Birkhead & Pizzari, 2002), as well as improved methods for quantifying selection (Arnold & Wade, 1984; Shuster & Wade, 2003). Advances in theoretical and empirical research have further enriched our understanding of sexual selection by highlighting the roles of condition dependence (Cotton et al., 2006), context dependence (Cornwallis & Uller, 2010; Qvarnström, 2001) and ecological factors (Miller & Svensson, 2014). Despite this growing complexity, classical sexual selection theory remains powerful in its simplicity.

The basis of sexual selection is widely accepted to lie in anisogamy, the asymmetry in gamete size and energetic investment between the sexes (Parker et al., 1972). Females typically produce fewer, larger, and energetically costly gametes (eggs), while males produce numerous small and less expensive gametes (sperm) (Hayward & Gillooly, 2011). This asymmetry imposes distinct reproductive constraints: female reproductive success is generally limited by egg production and parental investment, while male reproductive success is more often constrained by the number of mates they can successfully fertilize (Bateman, 1948; Parker et al., 1972; Trivers, 1972). These differences in gametic investment and reproductive constraints drive the evolution of sex-specific mating strategies (Schärer et al., 2012; Trivers, 1972). Traditionally, females have been portrayed as the choosy sex, selecting for male traits associated with individual quality, whereas males seek to mate with as many females as possible to maximize their reproductive success (Janicke et al., 2016). However, recent research emphasizes the nuance in these roles and increasingly acknowledges female-female competition and male mate choice, even in non-sex-reversed role species (Edward & Chapman, 2011; Stockley & Bro-Jørgensen, 2011). Despite this flexibility, because access to females becomes a limiting factor for male reproductive success, intense intrasexual selection often arises among males (Clutton-Brock & Vincent, 1991). This competition frequently generates a reproductive skew where only a few males mate with multiple females, while numerous others remain unmated (Hager & Jones, 2009). As a result, male reproductive success typically exhibits greater variance than that of females (Bateman, 1948; Shuster & Wade, 2003).

To gain access to multiple females, males can maintain mating groups, and in female-defence polygyny, this involves directly defending clusters of females (Emlen & Oring, 1977). This strategy is common among ungulates, where a high-ranking male defends a group of females, mating with them as they come into estrus (Bowyer et al., 2020) (e.g. reindeer, *Rangifer tarandus* (Hirotani, 1994); waterbuck, *Kobus ellipsiprymnus* (Wirtz, 1982); plains zebra, *Equus burchellii* (Fischhoff et al., 2007)). These groups are traditionally called harems, but hereafter we use the term *mating group* to describe this social structure.

Changes in the size and composition of mating groups are common and result from interactions between males and females. Females may leave and rival males can take control through serious fights (Body et al., 2015; Bowyer et al., 2020). To maintain group cohesion, high-ranking males herd females to keep them aggregated (Body et al., 2014; Walther, 1991). They also attempt to prevent subordinate males, frequently remaining on the periphery, from joining and achieving copulations through opportunistic behaviour (Espmark, 1964a; Schradin, 2022). Females, for their part, frequently move between mating groups, a behaviour believed to assist in assessing different potential mates (Body et al., 2015; Byers et al., 1994). While some studies suggest a preference for high-ranking males (Clutton-Brock & McAuliffe, 2009; Hirotani, 1989), females may not consistently exhibit such preferences (Stopher et al., 2011). Females may also join mating groups to avoid harassment from subordinate males. (Bro-Jørgensen, 2011; Hirotani, 1994).

Underlying these dynamics is the dominance hierarchy among males, which largely determines access to mating groups and reproductive success. Rank is associated with age, body size, body mass, and size and complexity of antlers, with older and stronger males typically achieving higher positions (Barrette & Vandal, 1986; McCullough, 1971; McElligott et al., 2001). High-ranking males usually monopolize the majority of matings, while subordinates secure only limited opportunities (Bowling & Touchberry, 1990; Hirotani, 1994). Hierarchies are not static: condition loss can lead to shifts in rank and turnover of mating group ownership within a single mating season (Holand et al., 2012; McCullough, 1971; Pintus et al., 2015).

The mating season incurs a variety of costs, primarily in terms of energy (Daly, 1978). Mating behaviours may incur substantial energetic costs through direct metabolic costs, but also by compromising the individual's ability to engage in other important activities such as feeding (Griffiths, 1996; Robinson & Doyle, 1985; Sparkes et al., 1996). Additionally, mating comes with risks. It can increase vulnerability to predation (Magnhagen, 1991) and raise the risks of disease transmission (Kokko et al., 2002). Aggressive interactions often occurring during the mating season, such as fighting, can also be costly in terms of injuries (Geist, 1986; Johnstone & Keller, 2000) and could even lead to death (Wilkinson & Shank, 1976).

Individuals are expected to minimize these costs by allocating their mating effort strategically (Breedveld & Fitze, 2016; Ramm & Stockley, 2014). To maximize their reproductive success, males often show a preference for females with higher fecundity (Bonduriansky, 2001; Jones et al., 2001; Sargent et al., 1986). Female fecundity is frequently associated with phenotypic traits such as size (Honěk, 1993; Prado & Haddad, 2005) and body mass (Kuramoto, 1978; Sand, 1996). Yet, successful fertilization depends not only on mate quality or the act of copulation itself, but also on appropriate timing. For a wide range of mammals, females must be in a state of sexual receptivity called estrus to accept mating and be capable of conceiving (Boness, 2009). Species vary in the number of estrous cycles they undergo per mating season, ranging from one to multiple; moreover, receptivity is restricted to the estrous phase, which represents a brief window within each cycle (Scheun, 2018). Mating outside this window is unlikely to result in fertilization and may, on the contrary, be disadvantageous due to the associated costs. Consequently, males are expected to strategically focus their mating effort on females in estrus, while females may also modulate their activity according to their reproductive status. Thus, variation in reproductive status may alter behavioural interactions.

It follows logically that female behaviour would shift across the reproductive cycle, given its regulation by underlying hormonal processes. Fluctuations of gonadal steroid hormones (or sex hormones), particularly androgens, estrogens, and progesterone, seem to impact not only receptivity but also sexual arousal and behaviour (Jennings & de Lecea, 2020; Pfaus et al., 2015). Some studies have shown that estrus and the accompanying rise in estrogen levels are frequently associated with a decrease in feeding (Brobeck et al., 1947; Wade, 1972; Yoest et al., 2019) and an increase in locomotion activity, which facilitates mate location as well as the production and detection of social signals (Anantharaman-Barr & Decombaz, 1989; Cushing et al., 1995; Ervin et al., 2015; Mičiaková et al., 2024). These findings suggest that hormonal state may modulate behavioural priorities in ways that favour reproductive activity during estrus.

These hormonal changes can, in turn, alter the production and composition of pheromones, conspecific chemical signals emitted by an individual that elicit a specific response from the receiver (Karlson & Lüscher, 1959). In many species, the chemical profile of the female shifts with mating status, although this has been most extensively characterized in insects (Gomez-Diaz & Benton, 2013; Thomas, 2011). One key function of these chemical signals is to convey information about sexual receptivity and fertility (Coombes et al., 2018). Certain chemical compounds have been found to be emitted only by female ungulates in estrus through urine (Archunan & Rajagopal, 2013; Ramesh Kumar et al., 2000), feces (Sankar & Archunan, 2008) and vaginal secretions (Jemiolo et al., 1995). Additionally, secretions from specialized scent glands can contribute to attracting the opposite sex and potentiating mating behaviour (Eisenberg & Kleiman, 1972).

Detection of female sexual receptivity in mammals relies primarily on olfaction. Chemical signals are perceived through two complementary chemosensory systems: the main olfactory system and the accessory olfactory system (Tirindelli et al., 2009). The vomeronasal organ, a key structure of the accessory olfactory system found in most mammals, is believed to function as a specialized chemoreceptor of sex pheromones and thus facilitates the detection of estrus in females (Estes, 1972; Igbokwe, 2009). The vomeronasal organ is closely associated with the flehmen response, a behaviour commonly observed in felids and ungulates, in which males curl their upper lip to move fluids, often urine, from the oral cavity into the vomeronasal organ (Eisenberg & Kleiman, 1972; Müller-Schwarze, 1991). Additional mating behaviours in ungulates that reflect the investigation of female receptivity include sniffing, licking and nuzzling the anogenital region as well as inspecting feces or licking urine from the ground or directly from the female as she urinates (Bergerud, 1974; Grau, 1976; Müller-Schwarze et al., 1979).

Numerous studies across invertebrates and vertebrates demonstrate males' ability to distinguish virgin from non-virgin females, and unmated from mated females, with most experiments reporting a preference for virgins and unmated individuals (Richardson & Zuk, 2024; Thomas, 2011). This body of research is heavily skewed toward insects and arachnids, where sperm competition is a prominent selective force thought to favour males that can detect female mating status (Edward &

Chapman, 2011; Lewis & Iannini, 1995; Morse, 2010). In vertebrates, behavioural studies examining female reproductive status, such as estrous condition or mating history, are comparatively limited and concentrated on a few groups: rodents, which have served as the main model system (Ferguson et al., 1986; Huck & Banks, 1984; Moulin et al., 2021; Zinck & Lima, 2013); primates, where attention has centered on male's response to female fertility cues (Engelhardt et al., 2004; Reichert et al., 2002); and domestic livestock, where research is largely frame within an animal science context, emphasizing hormonal regulation of sexual behaviours for reproductive management (D'Occhio & Brooks, 1980; Fritz et al., 2019). Overall, behavioural ecological studies of how female reproductive status influences mating dynamics remain scarce, particularly in natural settings.

Reindeer provide a particularly suited model for studying the influence of reproductive status on mating behaviour. They are both highly polygynous and seasonal breeders, with a short, well-defined rut during which females are in estrus for only 24-48 hours (Bergerud, 1975; Espmark, 1964a; Ropstad, 2000). This narrow window, combined with the high energetic costs of maintaining a mating group and securing copulations (Barboza et al., 2004), likely creates strong selective pressure on both sexes to optimize their mating investment. During the rut, males engage in conspicuous behaviours, which are readily observable in the field. Moreover, mating groups are structured around clear dominance hierarchies, offering an opportunity to investigate mating behaviours within a defined social context. Furthermore, investigating whether males preferentially target unfertilized females can provide insight into male mate choice, an underexplored aspect of reproductive behaviour in a classic system of intense male-male competition.

The thesis aims to investigate whether female reproductive status (fertilized vs. unfertilized) influences mating behaviour in reindeer. Using a field-based experimental design in which males had simultaneous access to both fertilized and unfertilized females, we recorded male and female behaviour, enabling us to examine not only individual-level behaviours, but also mating group composition, spatial positioning and the influence of male rank. Specifically, we tested four predictions:

(1) Males would display a higher frequency of mating behaviours toward unfertilized females compared to fertilized females.

(2) Unfertilized females would exhibit distinct activity budgets, characterized by increased walking and standing compared to fertilized females.

(3) The proportion of unfertilized females would be higher within mating groups than in the population as a whole, and even higher within the core areas of these groups.

(4) Both the proportion of mating behaviours toward unfertilized females and the proportion of unfertilized females in the core areas would decrease with male rank.

2. Methods

2.1 Study site and population

The study was conducted on a semi-domesticated reindeer population at the Kutuharju Reindeer Research Station, in Kaamanen, Finland (69°N, 27°E) in 2003. The study was carried out in two large enclosures (Lauluvaara, 13.8 km^2 and Sinioivi, 15 km^2), where reindeer could roam and associate freely in an area characterized by birch (*Betula* spp.) and pine (*Pinus sylvestris*) forests with many bogs and lakes. Reindeer were individually identifiable by numbered, colour-coded collars. Males were fitted with VHF radio collars, enabling us to track them.

2.2 Experimental design

During the first estrous period of 2003, the herd was split into two groups. Half of the females (n=51) were maintained with 4 vasectomized males in the Lauluvaara enclosure, while the other half (n=50) were kept with 4 fertile males in the Sinioivi enclosure. The males in both enclosures had the same age structure: one 1.5-year-old, one 2.5-year-old old and two 3.5-year-olds. Female age and weight structure were also kept similar between treatments. As seasonally polyestrous animals, female reindeer can have a subsequent estrus 13-33 days after the initial ovulation cycle (Ropstad et al., 1995). For the second estrous period, all females were merged with the 4 fertile males in the Sinioivi enclosure. Calving dates and paternity testing allowed us to verify if females in Sinioivi had been fertilized during their first estrus, as well as if those in Lauluvaraa remained unfertilized. Calving dates revealed that three females in Sinioivi had not been fertilized during their first estrus, and DNA marker analysis revealed that the vasectomy procedure failed for two males, resulting in 13 females expected to be unfertilized having already conceived. Consequently, at the beginning of the second estrous period, there were 60 fertilized and 41 unfertilized females.

2.3 Data collection

The second estrous period, defined as the interval from 24 October until 4 November 2003, was monitored from approximately 10:00 to 17:00 each day. All four males and their mating group, if they had one, were observed daily, ensuring a consistent observation effort across males. As the reindeer were accustomed to humans, close observation was feasible without causing disturbance.

Focal instantaneous sampling (Martin & Bateson, 2007) was used to record activity budgets and mating behaviours of individuals. One focal observation consisted of recording the activity (feed, rest, stand, walk or other (mating behaviour)) of one individual every 15 seconds for 15 minutes, for a total of 60 observations per focal. Mating behaviours directed to a single female were classified into three categories: investigating, herding and courting. Investigating comprises a male's effort to determine whether a female is in estrus (lick, sniff, flehmen). Herding corresponds to a male's attempt to control a female's movement until she returns to the mating group (herd, chase). Courting corresponds to a male spending time close to a female, showing sexual activities such as mounting and following. The frequencies of investigating, herding, and courting were combined to calculate the overall frequency of mating behaviours.

The composition of mating groups was assessed by visually identifying all individuals present. A mating group was defined as a group of individuals that are spatially separated from others and exhibit coordinated behaviours such as moving, resting or feeding together (Lent, 1965), with at least one sexually mature male and female present. In each group, a mating group holder (or dominant male) was also designated, which is easily identified in reindeer as he exhibits clear control over the females. Subordinate males tend to stay on the periphery of the mating groups. Male rank was determined based on observations of agonistic and intersexual interactions (Tennenhouse et al., 2011). The core area of a male was defined as a 10-meter radius circle centred on him. Individuals within core areas were recorded, and only records separated by a minimum interval of 30 minutes were retained, to allow for group remixing. Core areas in which 25% or more of the individuals were not identified were excluded from analysis. The core area of a dominant male was considered to be the core area of the corresponding mating group, as he is usually positioned at its centre.

Copulation events were recorded ad libitum, including the date and the IDs of the individuals involved. During the following calving season, the birth date of all newborns was recorded, and blood samples were collected for paternity analysis. For females from the unfertilized group that were not observed mating, copulation dates were estimated using a backdating technique. The mean gestation length (211 days) for the second estrous period was calculated from 6 females for which both the copulation date and the calving date were recorded. This average was then subtracted from calving dates to estimate copulation dates. For the 4 females that did not give birth the following year, it was assumed that they had not been fertilized. For the 6 individuals that were killed before the calving season, it was assumed they had been fertilized, as the majority of females conceive during the rut (Rowell & Shipka, 2009). Since calving dates were unavailable for these individuals, they were assigned the average copulation date based on 8 observed copulations. This approach was considered acceptable, given that female *Rangifer* exhibit a brief and highly synchronous estrous period (Bott, 2017; Dauphiné & McClure, 1974).

The estimated copulation dates provided a more accurate assessment of each female's reproductive status. A female was classified as unfertilized until the day she was mated; from the following day onward, her status was considered fertilized. This method also allowed us to calculate the daily proportion of unfertilized females at three spatial scales (core area, mating group and population).

2.4 Statistical analysis

All analyses were carried out in the program R version 4.3.3, with the significance level set as 0.05 (R Core Team, 2024). As a sensitivity check, analyses were re-run excluding the 6 individuals assigned the average copulation date, which did not significantly change the results.

2.4.1 Male behaviour

We analyzed male mating behaviours frequency using a Generalized Linear Mixed Model (GLMM) with a Poisson error distribution and a log link function, appropriate for count data. The response variable was the number of mating behaviours performed by a male toward a specific female, summed daily. Only observed male–female interactions were included. To test whether male courtship behaviour was influenced by female reproductive status, we included female reproductive status (categorical variable with two levels: fertilized and unfertilized) as a fixed effect in the model and controlled for temporal trends by adding time (in days) as an additional fixed effect. To account for repeated observations of individuals across multiple pairings, we included male and female identities as random effects. We also included the log of the number of females in each reproductive status group per day as an offset in the model to control for the unequal number of females across reproductive statuses. To verify that the observed effect of female reproductive status was not confounded by male-female familiarity (i.e. females from Sinioivi being familiar and those from Lauluvaara unfamiliar), we conducted a complementary analysis restricted to unfamiliar females only, and results did not significantly differ.

We examined each mating behaviour category (herding, investigating, and courting) separately to test whether males directed these behaviours more frequently toward unfertilized females. Because the daily proportion of unfertilized females varied, we calculated an expected proportion of unfertilized females for each day and computed a weighted average across days, weighting it by the number of behavioural observations recorded each day for each behaviour category. This provided a mating behaviour-specific expected proportion of unfertilized females under the null hypothesis of no preference. Given the small sample size and limited repeated observations, one-tailed binomial tests were used to determine whether the observed proportion of unfertilized females receiving each type of mating behaviour exceeded the expected proportion.

2.4.2 Female behaviour

We assessed the influence of reproductive status on female activity budgets using a GLMM fitted with a negative binomial type 1 (NB1) error structure and a log link function. The model included female reproductive status, activity type (categorical variable with four levels: feed, rest, stand and walk) and their interaction as fixed effects. Female identity was included as a random effect and the total number of observations per focal was incorporated as an offset to account for variation in sampling effort. Several model families were explored, and the NB1 provided the best overall fit based on diagnostic checks, despite exhibiting slight underdispersion. We used Type III Wald chi-square tests with sum-to-zero contrasts to ensure proper estimation of main effects and their interaction.

2.4.3 Mating group

To test whether the proportion of unfertilized females varied across spatial scales, we fitted a GLMM with a binomial error structure and a logit link function. Spatial scale (categorical variable with three levels: core area, mating group and population) was included as a fixed effect, along with time, to account for the temporal decline in unfertilized females over the course of mating. To control for pseudoreplication due to repeated sampling in the population and mating groups, we included a single random effect that assigned unique IDs to each of the daily population, mating groups and core areas. Only the core areas of dominant males were included in the analysis (i.e. to compare the core areas of mating groups to the mating groups themselves). We conducted post hoc pairwise comparisons using Tukey-adjusted contrasts to evaluate differences among spatial scales.

2.4.4 Male rank

We were unable to directly assess the effect of male rank on the proportion of mating behaviours directed toward unfertilized females due to limited sample sizes. Instead, we compared the proportion of mating behaviours directed toward unfertilized females between the males of various ranks. Accordingly, all pairwise comparisons between male ranks were performed using one-tailed Fisher's exact tests, testing the hypothesis that higher-ranking males exhibited more mating behaviours than lower-ranking males. P-values were adjusted for multiple comparisons using the Holm correction.

To examine the influence of male rank on the spatial positioning in relation to female reproductive status, we used a GLMM with a binomial error structure and a logit link to compare the proportion of unfertilized females across male ranks, focusing on the core area level. This spatial scale was selected based on observed differences in the proportion of unfertilized females across spatial scales (see Results). Male rank was included as a fixed effect, as well as the number of males present in the mating group, to account for potential variation in the social environment that could influence male access to unfertilized females. Mating group ID was included as a random effect to control for non-independence, as multiple core area observations originated from the same group.

3. Results

3.1 Male behaviour

Males exhibited significantly more mating behaviours toward unfertilized females than fertilized ones, with approximately a sevenfold increase in the frequency of these behaviours (GLMM, $\beta = 1.923$, SE = 0.370, $p < 0.001$; Figure 1). Additionally, the frequency of mating behaviours increased over time (GLMM, $\beta = 0.206$, SE = 0.050, $p < 0.001$; Appendix A). When the analysis was restricted to unfamiliar females, the effect of reproductive status on male mating behaviours remained significant (GLMM, $\beta = 1.930$, SE = 0.406, $p < 0.001$). This indicates that, even when controlling for familiarity, female reproductive status alone influences male mating behaviours.

When analyzed separately, the three mating behaviour categories showed distinct patterns of male preference for unfertilized females (Figure 2). Courtship behaviours were exclusively directed toward unfertilized females (22 of 22 observations), significantly exceeding the expected proportion (0.21) (one-tailed binomial test, $p < 0.001$). Similarly, males directed a significantly greater proportion of investigations toward unfertilized females than expected (one-tailed binomial test, $p < 0.001$). In contrast, herding did not exceed random expectation and was more balanced between fertilized and unfertilized females (one-tailed binomial test, $p = 0.16$).

3.2 Female behaviour

To examine whether female activity budgets changed with reproductive status, we fitted a GLMM including an interaction between activity type and reproductive status. The interaction term was not statistically significant (Wald $\chi^2 = 1.786$, df = 3, $p = 0.62$), nor was the main effect of reproductive status (Wald $\chi^2 = 0.065$, df = 1, $p = 0.80$), suggesting that the overall activity budgets of fertilized and unfertilized females were similar. In contrast, activity type was highly significant (Wald $\chi^2 = 168.519$, df = 3, $p < 0.001$), indicating strong differences in counts across activity types regardless of reproductive status. Accordingly, the average frequencies of feeding, standing, walking and resting across all females were 34.67 ± 3.54 (SE), 11.56 ± 1.64 (SE), 7.31 ± 1.16 (SE) and 1.73 ± 0.48 (SE), respectively (Figure 3).

3.3 Mating group

The proportion of unfertilized females varied across spatial scales. It was significantly higher in the core areas compared to both the mating groups (estimated difference = 0.638, SE = 0.167, $p < 0.001$) and the entire population (estimated difference = 0.603, SE = 0.186, $p < 0.004$), with no significant difference between the latter two ($p = 0.98$; Figure 4). The mean proportion of unfertilized females was 0.36 ± 0.03 (SE) in the core area, 0.23 ± 0.02 (SE) in the mating group and 0.24 ± 0.02 (SE) in the population.

3.4 Male rank

The first- and second-ranked males each performed 26 mating behaviours. The rank 1 male directed all his mating behaviours exclusively toward unfertilized females, whereas the rank 2 male directed half of his mating behaviours toward unfertilized females. Lower-ranking males (ranks 3 and 4) displayed very few mating behaviours, with only three each. The rank 1 male courted significantly more unfertilized females than both the males ranked 2 and 4 (one-tailed Fisher's exact test,

$p < 0.001$ and $p = 0.001$ respectively; Figure 5). No other comparisons between higher and lower ranking males were significant (one-tailed Fisher's exact test, all $p > 0.05$).

The proportion of unfertilized females in the core area decreased with male rank (GLMM, $\beta = - 0.516$, SE = 0.129, $p < 0.001$; Figure 6). In addition, the number of males in the mating group had a significant negative effect on the proportion of unfertilized females in a male's core area (GLMM, $\beta = -0.331$, SE = 0.131, $p = 0.012$).

4. Discussion

4.1 Male behaviour

Female reproductive status influenced the frequency of male mating behaviours. This not only suggests that males can distinguish between females according to their reproductive status, but the strong effect size also indicates that they preferentially direct mating effort toward unfertilized females. Such a preference likely reflects a strategy to optimize mating investment, since investing in fertilized females would not increase fitness and may even impose costs in terms of energy expenditure or missed mating opportunities, particularly in species that do not store sperm (Kelso & Verrell, 2002). Studies have demonstrated that males exhibit mate choice for females of higher fecundity, and in some cases allocate greater mating effort toward them (Byrne & Rice, 2006; Jones et al., 2001; MacLeod & Andrade, 2014). Male mate choice has also been shown to result in higher reproductive success and increased fitness payoffs (Chen et al., 2012; Jordan et al., 2014).

There is growing recognition that male mate choice occurs broadly across diverse taxa (Edward & Chapman, 2011). Male mate choice may arise when there is variation in female quality, and when the benefits of selecting among females outweigh the costs of assessment (Andersson, 1994; Parker, 1983). The likelihood of male mate choice depends on mating investment, the expenditure of resources such as time and energy in each mating event (Bonduriansky, 2001; Edward & Chapman, 2011). High mating investment tends to favour choosiness. Male mate choice is more likely to occur when the number of available females exceeds a male's mating capacity (Edward & Chapman, 2011), such as when females are encountered simultaneously rather than sequentially, restricting a male's ability to mate with all of them (Barry & Kokko, 2010), or when sperm becomes a limiting resource (Dewsbury, 1982).

Several aspects of reindeer reproductive ecology create conditions that may favour male mate choice. First, males invest heavily in mating, sometimes losing more than 20% of their body weight during the rut (Kojola, 1991; Mysterud et al., 2003). Second, because females aggregate in mating groups, males encounter many simultaneously, and the number of females present could exceed a male's physical ability to mate with all available partners, creating the potential for choosiness. Although sperm depletion has not been demonstrated in reindeer, it remains a plausible constraint as the rut progresses, as shown in another ungulate (Preston et al., 2001). Our result, showing that males display more mating behaviours toward unfertilized than fertilized females, is therefore consistent with the idea that even in highly competitive mating systems, males may exhibit mate choice.

As highlighted by Edward and Chapman (2011), not all traits targeted by mate choice are necessarily heritable. This applies to traits yielding direct benefits, such as reproductive status, a condition that all females express, but at different times (Edward & Chapman, 2011). Consequently, although such traits may be favoured by mate choice, they do not generate an evolutionary response in females. Similarly, as shown previously, mating status and age (Mainguy et al., 2008; Muller et al., 2006) are also non-heritable traits that can influence male mate choice without producing evolutionary change in the chosen sex.

Courting was observed exclusively toward unfertilized females, suggesting that males can reliably discriminate female receptivity before investing in energetically costly mating attempts. In reindeer, courtship involves prolonged close following, which is time-intensive, and its restriction to unfertilized females indicates a high degree of selectivity in male mating effort. Indeed, dominant male reindeer have been found to court more frequently the unmated than mated females (Kojola, 1986). Similar patterns have been reported in other species. For instance, male guppies follow, attempt copulations and copulate more with virgin females (Guevara-Fiore et al., 2009), male chameleons are more likely to court and mate with receptive females (Kelso & Verrell, 2002), and male long-tailed macaques show increased interest in females during or around the fertile phase (Engelhardt et al., 2004).

The complete absence of courtship toward fertilized female reindeer could reflect either sensitivity to the presence or absence of estrous signals, or detection of post-copulatory or fertilization-related changes. The higher proportion of investigation behaviours, such as sniffing and licking, directed toward unfertilized females suggests pheromone activity (Müller-Schwarze et al., 1979). In many ungulates, hormonal changes across the estrous cycle alter the chemical composition of vaginal mucus and urine. (Archunan & Rajagopal, 2013; Jemiolo et al., 1995; Ma et al., 1995; Rajanarayanan & Archunan, 2011). Sex pheromones present in urine and vaginal mucus have been shown to elicit male mating behaviours such as flehmen and mounting (Archunan & Rajagopal, 2013; Archunan & Ramesh Kumar, 2012; Klemm et al., 1987; Nishimura et al., 1991; Rajanarayanan & Archunan, 2011; Sankar & Archunan, 2004). Alternatively, post-copulatory mechanisms may contribute to males investigating a higher proportion of unfertilized females. Thomas (2011) identifies three pheromone-based explanations whereby females may produce repellent pheromones after mating, cease releasing attractant pheromones, or receive male-applied chemicals during copulation that subsequently alter their attractiveness. The investigation behaviours observed in reindeer may therefore reflect male assessment of chemical differences, allowing them to identify estrous females and adjust mating effort accordingly.

However, investigation does not appear to serve solely to determine female reproductive status. If its only function were to assess receptivity, males would be expected to investigate fertilized and unfertilized females in similar proportions. Instead, the observed pattern suggests that once males detect that a female is in estrus, they intensify their investigation, possibly to confirm the signal. This repeated investigation may also represent an early stage of courtship, functioning as a way for males to signal their interest to the female (Mossing & Damber, 1981).

Herding was the only mating behaviour in which males did not show a bias toward unfertilized females. This contrasts with Hirotani (1989), who reported that dominant males herded pre-conception females more frequently than post-conception ones. Moreover, Bergerud (1974) observed that estrous females were herded more vigorously. One possible explanation for our result is that investigation and courtship occur at a closer range, allowing males to assess a female's reproductive status. Herding, in contrast, usually involves females at a greater distance on the periphery of the mating group. Because dominant males usually herd females as soon as they tend to leave the group (Espmark, 1964a), they may have little time to evaluate reproductive status before deciding whether to herd them back.

Beyond these distance and time constraints, males may herd any females simply to increase group size, thereby increasing the likelihood of including more estrous females. In other polygynous ungulates and primates, males with larger mating groups tend to have a higher reproductive success (Gibson & Guinness, 1980; Modig, 1996; Robbins et al., 2014; Xia et al., 2021). Maintaining group size could also be advantageous if mating group size influences females. Female fallow deer tend to join males that have large mating groups (Clutton-Brock et al., 1989; Clutton-Brock & McComb, 1993). A similar interest in remaining in larger groups has been suggested in reindeer (Body et al., 2015). Such preferences may arise either through mate choice copying or through a general attraction to larger aggregations. Under either scenario, males that maintain larger groups would appear more attractive simply by having more females. Thus, by herding any females attempting to leave regardless of their reproductive status, males may not only retain potential mates, but also potentially increase their attractiveness to females.

Furthermore, sperm competition could motivate males to herd fertilized females. In reindeer, many females (42%) mate with more than one male during the rut (Coombs et al., 2023). Although detailed studies of sperm competition are limited in this species, keeping fertilized females in the group may benefit the dominant male by limiting mating opportunities for rival males and reducing sperm competition.

4.2 Female behaviour

Our prediction that unfertilized females would exhibit higher levels of walking and standing was not supported. The absence of detectable differences in activity budgets between fertilized and unfertilized female reindeer suggests that reproductive status has a limited influence on daily behavioural allocation. However, several studies on ungulates report contrasting patterns, with reproductive status associated with clear behavioural changes. Cattle exhibit increased locomotor activity and reduced feeding time during estrus (Mičiaková et al., 2024; Pahl et al., 2015; Underdahl et al., 2018), and white-tailed deer *(Odocoileus virginianus)* show a rise in movements during proestrus (one to two days before mating) and estrus (Ozoga & Verme, 1975). In female reindeer, Kojola (1986) found differences in activity budgets between estrous and anestrous females, with estrous females having a tendency to stand more and lie down and feed less. In that study, “estrous females” were defined as females observed during the five hours preceding mating. The discrepancy with our results may reflect differences in observation timing, suggesting that shifts in activity budgets occur within a narrow window around estrus, rather than earlier, as in our broader “unfertilized” category.

Activity synchrony within mating groups may further account for the lack of differences in activity budgets observed between reproductive statuses. As in any aggregation of individuals, group cohesion depends on individuals being at the same place at the same time, which likely requires engaging in the same activity (Conradt & Roper, 2000). High within-group synchrony has been reported in both wild and captive caribou, and was maintained even during the rut, despite a slight reduction compared to other periods (Maier & White, 1998). By promoting cohesion, activity synchrony enables individuals to remain part of groups and thereby gain the benefits of group living, such as reduced predation risk (Kie, 1999; Molvar & Bowyer, 1994). Thus, during the rut, maintaining coordinated activity patterns may constrain individual variation in activity, even across females of different reproductive status.

Although not the primary focus of the present study, the overall female activity budget observed here differs from previous reports. In our study, feeding clearly dominates daily activity, whereas in other studies, time is more evenly split between resting and feeding (Boertje, 1985; Kojola, 1986). This discrepancy may be explained by differences in the methods used. Our observations were conducted primarily during daylight hours, while other studies also included dark periods. Reindeer are known to rest more during the night than during the day (Collins & Smith, 1989) and to feed primarily during the day (Erriksson et al., 1981), which could result in a relatively higher proportion of feeding recorded in daytime observations.

4.3 Mating group

Female reproductive status did not affect the overall composition of mating groups, as the proportion of unfertilized females within these groups closely matched that of the population as a whole. This aligns with our finding that males did not preferentially herd unfertilized females over fertilized ones. Despite male herding behaviour, females are able to leave the groups more or less freely (Hirotani, 1989). Fertilized females, however, did not appear more inclined to leave and tended to remain in the mating group. This contrasts with Kojola's finding (1986) that mated females were observed for longer periods outside mating groups.

Remaining in groups, even after conceiving, may nonetheless provide benefits such as reduced predation risk and improved foraging opportunities (Berger, 1978; Han et al., 2020; Kie, 1999). During the sampling period, predation pressure was unusually high, which likely reinforced females' tendency to remain clumped in mating groups, including fertilized individuals. This ecological context may help explain why the proportion of unfertilized females in mating groups did not differ significantly from that of the overall population. During the rut, staying in a mating group may also help females avoid harassment from subordinate males. Harassment levels tend to be higher when females are solitary (Clutton-Brock et al., 1992; Galimberti et al., 2000), suggesting that being part of a mating group can lessen these costs. This may occur through dilution effects in larger groups and through protection provided by dominant males, who often exclude or chase away rivals (Bro-Jørgensen, 2011; Carranza & Valencia, 1999; Clutton-Brock & McAuliffe, 2009).

Nevertheless, female reproductive status affected spatial positioning within mating groups, with unfertilized females being more concentrated in the core areas, suggesting that they may spend more time near dominant males. Comparable observations have been described in *Rangifer* by several authors. Bergerud (1974) noted that females in or approaching estrus frequently shifted locations to remain close to the dominant male, while Lent (1965) observed that the tended female typically occupied the center of the mating group. Espmark (1964a) reported that females in estrus constantly stayed in the vicinity of males, but moved away immediately after copulation. Furthermore, Kojola (1986) found that the average lying distance between a dominant male and an estrous female was 3.7 m (SE = 0.72), compared to 11.2 m (SE = 0.86) for an anestrous female. These observations align with our results, indicating that unfertilized females tend to be in the center of the mating groups close to the dominant male.

The higher proportion of unfertilized females in the core areas of the mating groups may result from both male and female behaviours, although it is likely driven primarily by the latter. Male herding behaviour functions to keep the mating group cohesive and to prevent individual females from straying (Walther, 1991). In other words, this behaviour is generally directed toward controlling the movement of females into and out of the mating group, rather than regulating their positions within it. Males also tend to maintain proximity to a single estrous female during courtship, which can temporarily alter her spatial behaviour and limit her movement (Walther, 1991). Nevertheless, in fission-fusion systems such as those observed in reindeer, females are known to move relatively freely within and between mating groups (Body et al., 2015; Hirotani, 1989). Therefore, the concentration of unfertilized females in the core area is more plausibly explained by female spatial patterns rather than direct male control.

This spatial pattern suggests that unfertilized females tend to stay closer to dominant males. Remaining near the male may help them signal their receptivity. Female mammals commonly advertise sexual receptivity via chemical signals (Coombes et al., 2018), which are likely to be more effective at close range. Additionally, male harassment can affect female movement (Clutton-Brock et al., 1992; Sundaresan et al., 2007). Staying near the group's core may partly reflect avoidance of the group's periphery, where the risk of male harassment by subordinate males can be greater (Galimberti et al., 2000). Consistent with this, Hirotani (1989) observed that subordinate males most often associated with females on the periphery of the group. Overall, female spatial positioning within the mating group may represent an adaptive strategy to maximize fertilization success with high-ranking males.

Beyond female reproductive status, various social and environmental factors may affect where females position themselves. For instance, females accompanied by a calf may spend less time in mating groups to reduce the risk of disturbance caused by intense male interactions, which can attack calves that come too close (Espmark, 1964a; Heatta, 2009). Social hierarchy may play a role, with high-ranking females being more capable of securing preferred positions, while subordinate individuals remain closer to the periphery (McMahon & Bradshaw, 2004; Sigg, 1980). Habitat characteristics, such as food availability and cover density, can also influence group distribution by affecting the safety and foraging opportunities (Hirth, 1977). Since these factors may not affect all females equally, they could add unaccounted variation that shapes the patterns observed between fertilized and unfertilized individuals.

4.4 Male rank

The highest-ranking male showed a markedly strong ability to direct mating behaviours toward unfertilized females, indicating a high degree of selectivity and efficient allocation of mating effort. Dominant male reindeer typically monopolize and defend their mating group (Hirotani, 1989). Their proximity to females probably allows them to better assess and discriminate among their reproductive statuses. Theoretical models further suggest that male mate choice may vary according to their quality (Pollo et al., 2022). High-ranking males, being both high-quality individuals and those facing the greatest mating costs (Hirotani, 1994; Mysterud et al., 2003), are therefore expected to be more selective.

Another pattern emerging from our results is that the proportion of unfertilized females increases in proximity to higher-ranking males. A similar trend was reported by l'Italien et al. (2012), who showed at the scale of the whole mating group that the social rank of dominant males was positively related to the number of females in estrus. High-ranking male reindeer tend to possess superior phenotypic traits, which are associated with greater reproductive success (Røed et al., 2007). Females may respond to dominance or traits reflecting it, indicating a preference for high-quality males (Berglund et al., 1996). Supporting this preference, female reindeer have been observed behaving aggressively toward young or lower-ranking males (Espmark, 1964b), suggesting active avoidance of lower-quality males. Similar female preferences for dominant males have been documented across many mammals (Clutton-Brock & McAuliffe, 2009).

In contrast, lower-ranking males exhibited very few mating behaviours, making it difficult to detect any preference for unfertilized females. Their behaviour likely reflects alternative mating tactics rather than an inability to distinguish between reproductive status. Because dominant males restrict their access to females, subordinates often rely on opportunistic tactics such as sneaky copulations when the dominant male is distracted (Holand et al., 2012; Røed et al., 2002). Under these circumstances, they may have little opportunity to assess the female reproductive condition, and their mating attempts may be driven more by immediate opportunities than by estrous signals. Subordinate males not discriminating between fertilized and unfertilized females is consistent with our previous result that fertilized females were not underrepresented in the mating group. Our result is similar to Kojola (1986), who reported that yearling males and male calves were the most active in mounting anestrous females.

5. Conclusion

This study demonstrates that female reproductive status plays a central role in shaping mating dynamics in reindeer. By examining both behaviour and spatial positioning, we show that mating interactions during the rut arise from strategies that are influenced by female reproductive status for both sexes. Males appear to invest their mating effort where it is more likely to yield reproductive returns, predominantly courting and investigating unfertilized females. While female activity budgets did not differ between reproductive statuses, changes in spatial positioning, specifically, closer proximity to dominant males, suggest that unfertilized females may make spatial choices to enhance their mating opportunities. High-ranking males, in turn, seem to benefit by preferentially directing mating behaviours toward unfertilized females and by attracting unfertilized females into their immediate vicinity.

These patterns highlight that sexual selection in reindeer operates through more than direct male–male competition. Even within a strong polygynous system, males show selective mating behaviours. In addition, it demonstrates the use of spatial strategies by females to increase reproductive opportunities with high-ranking males, suggesting that, although female mating behaviours may be less conspicuous, they still play a role in mating dynamics. This emphasizes the need for future research explicitly focused on female behaviours and their effect on mating interactions. Together, these insights underscore the importance of incorporating female reproductive state into analyses of mating systems and offer a framework for further exploring how individual condition shapes mating dynamics.

Figures

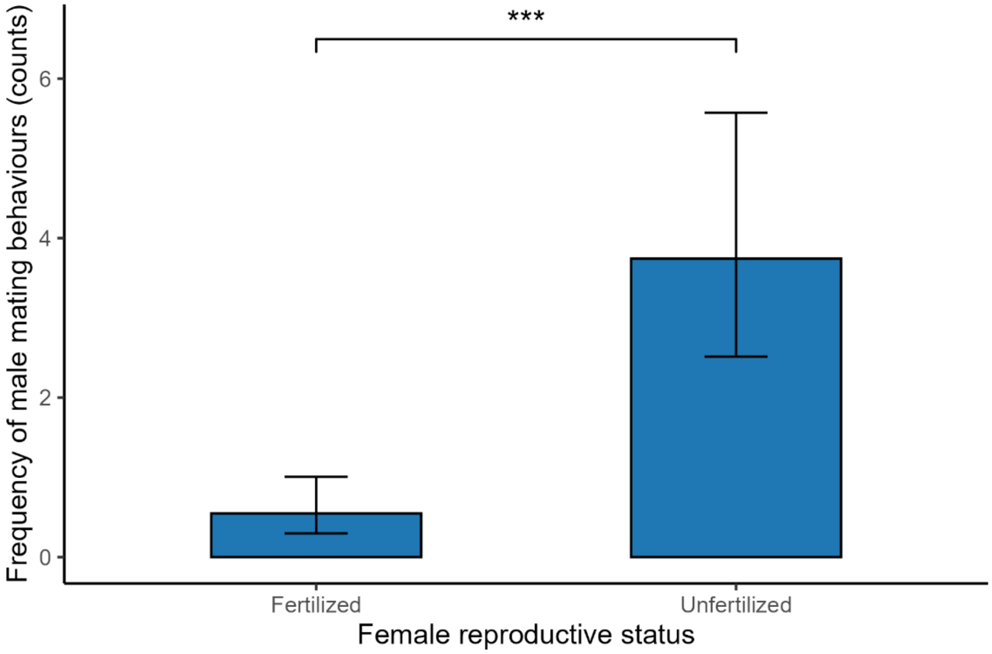

Figure 1: Model-predicted average frequency of male mating behaviours (± 95% CI bars) by female reproductive status in reindeer (*Rangifer tarandus*). Values are estimated marginal means based on data aggregated for each unique male-female pair observed per sampled day (n = 31 pair-by-day observations from 4 males and 27 females). Asterisks represent significant differences between fertilized and unfertilized females (α = 0.05).

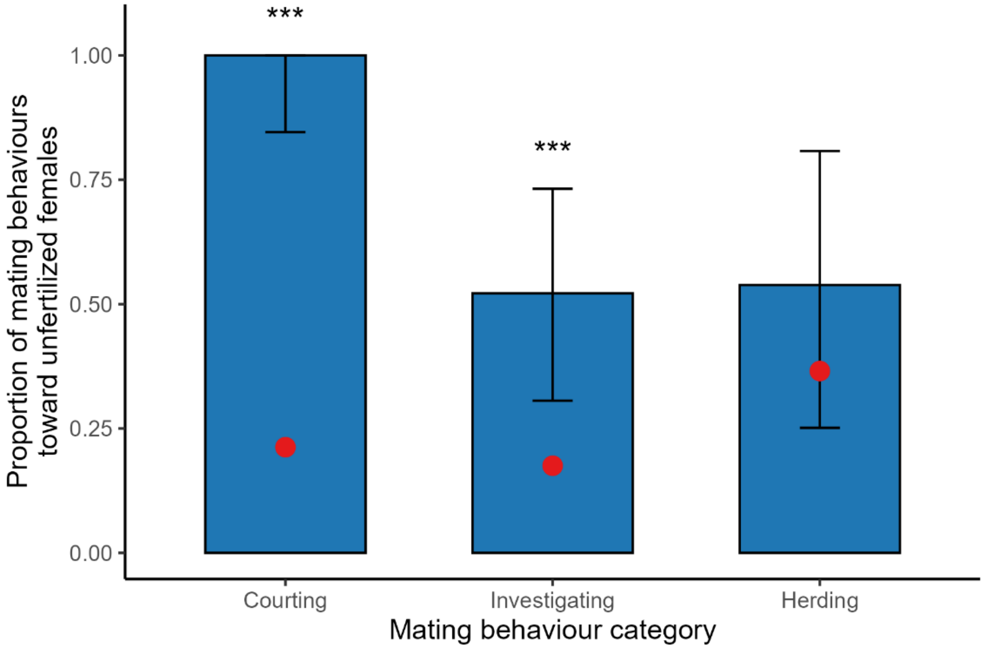

Figure 2: Average proportion of three mating behaviours (courting, investigating and herding) (± 95% CI bars) directed toward unfertilized female reindeer (*Rangifer tarandus*). Red dots indicate the expected proportion under the null hypothesis. Sample sizes: courting (n = 22), investigating (n = 23) and herding (n = 13). Asterisks represent significant differences between predicted and expected proportions (α = 0.05).

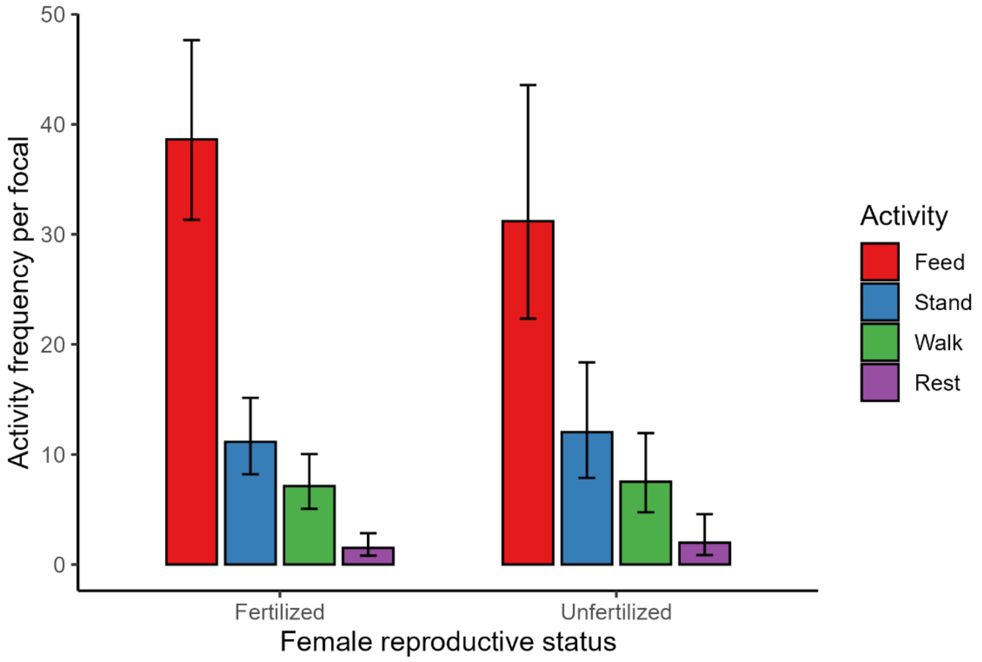

Figure 3: Model-predicted activity budget of fertilized and unfertilized female reindeer (*Rangifer tarandus*). Frequencies represent average activity counts per focal (60 observations) ± 95% CI bars and are derived from estimated marginal means. Sample size: n =51.

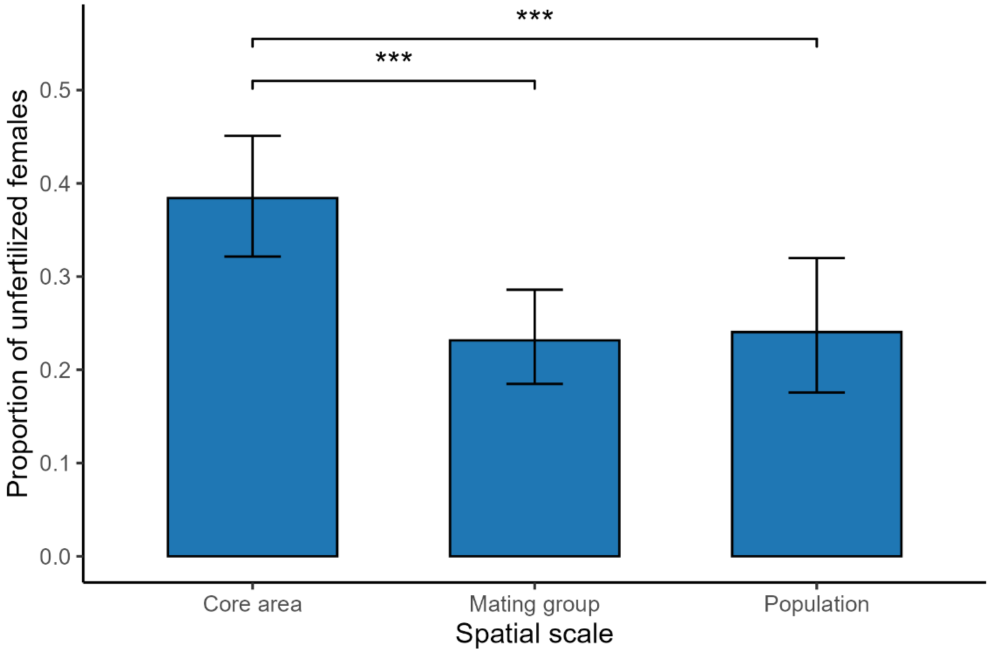

Figure 4: Model-predicted average proportion of unfertilized females (± 95% CI bars) across three spatial scales (core area (CA), mating group (MG) and population (POP)) in reindeer (*Rangifer tarandus*). Values are estimated marginal means based on observations involving 101 females. The dataset includes 80 CAs, each linked to one of the 29 MGs and one of the 12 POPs. Asterisks represent significant differences between levels of the spatial scale according to a Tukey-Kramer multiple comparisons test (α = 0.05).

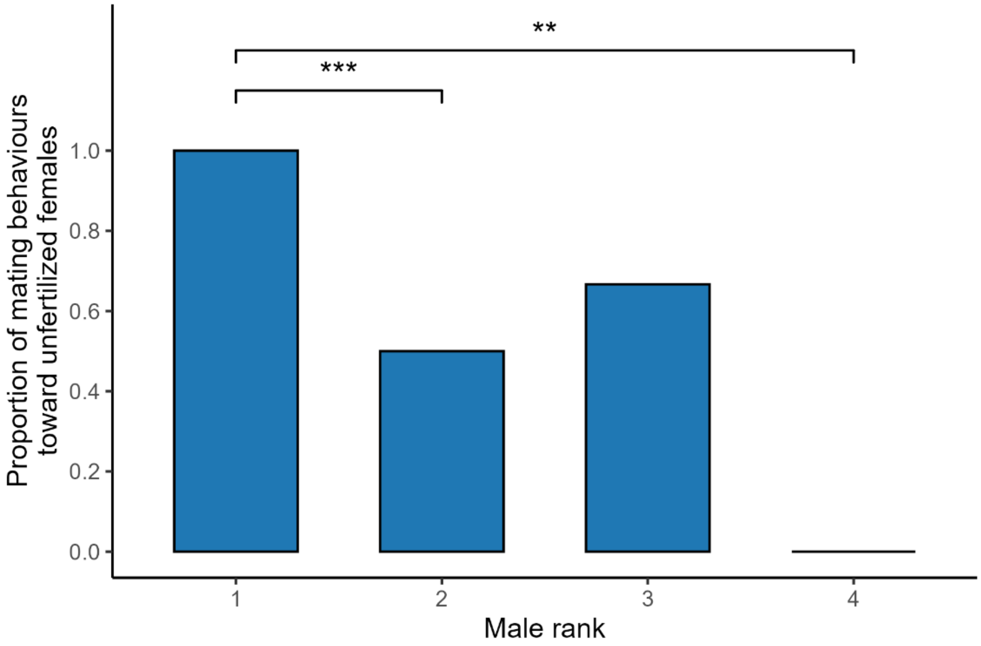

Figure 5: Proportion of mating behaviours directed toward unfertilized females shown by male rank in reindeer (*Rangifer tarandus*). Sample sizes (number of observed mating behaviours per individual male): rank 1 (n = 26), rank 2 (n = 26), rank 3 (n = 3) and rank 4 (n = 3). Asterisks represent a significant difference between male ranks with Holm correction (α = 0.05).

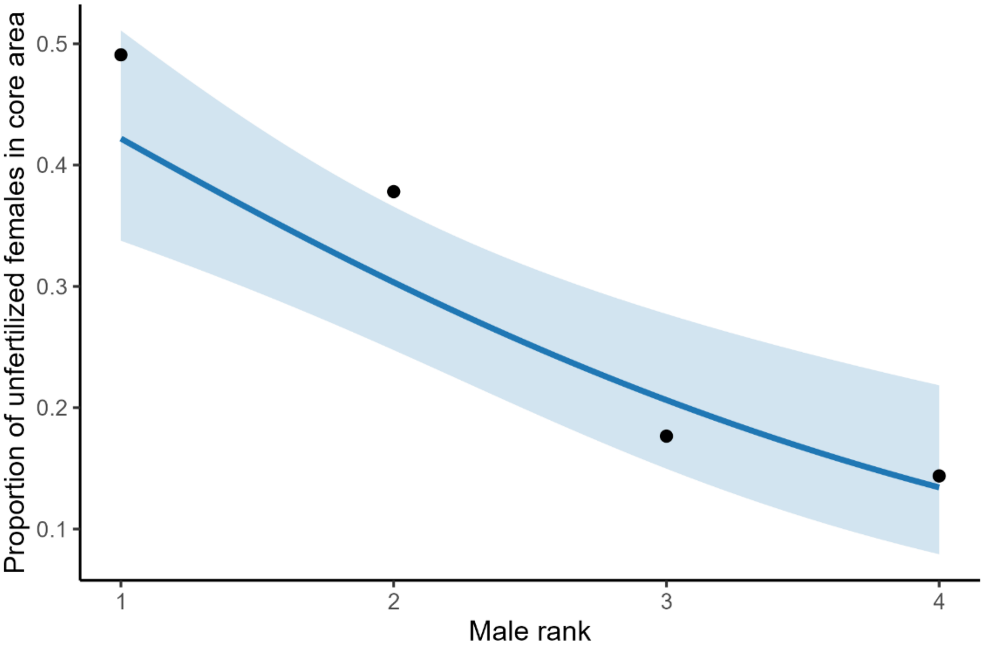

Figure 6: Model-predicted curve (with its 95% confidence interval band) depicting the proportion of unfertilized females in the core area across male rank in reindeer (*Rangifer tarandus*). Black dots represent the average proportion for each rank. Sample sizes (number of core areas per individual male): male 1 (n = 46), male 2 (n = 29), male 3 (n = 32) and male 4 (n = 16).

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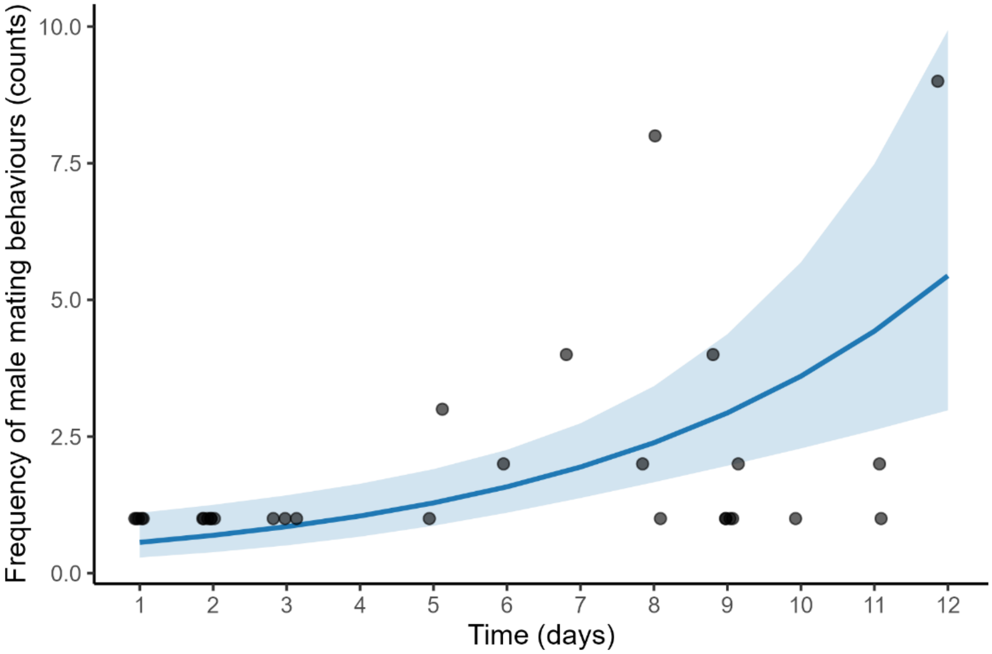
Appendix



Appendix A: Model-predicted curve (with its 95% confidence interval band) depicting the average frequency of male mating behaviours in reindeer (*Rangifer tarandus*) over the second estrous period of 2003 (24 October - 4 November). Black dots show the observed counts for each male-female pair per sampled day (n = 31 pair-by-day observations from 4 males and 27 females).