Mismatch between calf paternity and observed copulations between male and female reindeer: multiple mating in a polygynous ungulate?

Keenin R. Coombs[a], Robert B. Weladji[a,*], Øystein Holand[b], and Knut H. Røed[c]

[a]Department of Biology, Concordia University, 7141 Sherbrooke St. West, Montreal, QC, H4B1R6, Canada
[b]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, Oluf Thesens vei 6, 1433 Ås, Norway
[c]Faculty of Veterinary Medicine, Norwegian University of Life Sciences, Veterinærbygningen, Elizabeth Stephansens vei 15, N-1430 Ås, Norway

*Address correspondence to Robert B. Weladji. E-mail: robert.weladji@concordia.ca
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Abstract

In polygynous systems, such as that exhibited by reindeer *Rangifer tarandus*, mate choice can be difficult to disentangle from male intrasexual competition because male behavior may constrain female choice. Multiple mating may provide an avenue for female mate choice, though it is difficult to identify using behavioral estimators alone. Molecular techniques address this issue by affording ecologists an opportunity to reassess mating systems from a genetic perspective. We assessed the frequency and possible explanations for multiple mating in reindeer using a genetic approach to determine the success of observed copulations in a semi-domesticated herd in Kaamanen, Finland. Behavioral and genetic data were synthesized with population characteristics over a 7-year period to test the hypothesis that, if present, polyandry in reindeer is driven by sexual harassment from sub-dominant males. We observed multiple mating in 42% of females, with as many as 60% exhibiting multiple mating in certain years. We found no evidence that multiple mating resulted from sexual harassment by sub-dominant males, suggesting that it is likely a deliberate strategy among females. Conversion rate of copulations into paternities varied with male size, with smaller males more likely to experience mismatch than larger males. Female preference for larger males persisted despite the occurrence of multiple mating, possibly suggesting a mechanism for cryptic post-copulatory selection. We suggest further research to delineate the possible influence of cryptic post-copulatory selection and multiple mating to defend against infertility in exhausted males.

Key words: female choice, mate choice, mating systems, polyandry, reproductive success, sexual selection.

Polygyny, a mating system characterized by intense competition between males for access to females, has long been considered the dominant mating system among mammals (McEachern et al. 2009). In polygynous systems, males have generally been considered more active players than females, with individual variation in male reproductive strategies contributing to discrepancies in reproductive success among competitors (Trivers 1972; Røed et al. 2005; Clutton-Brock and McAuliffe 2009). Females have, conversely, been considered a limiting resource (Trivers 1972; Clutton-Brock and McAuliffe 2009). Consequently, the bulk of research on the reproductive ecology of polygynous species has traditionally addressed male behavior. More recently, an increasing body of literature has examined female mate choice.

Much existing literature on female mate choice has focused on birds and fish, possibly reflecting the conspicuousness of male reproductive displays among many species within these taxa (Clutton-Brock and McAuliffe 2009). In particular, sexually dimorphic ornamentation and/or coloration occur frequently among birds and fish; and are thought to primarily function as honest indicators of mate quality (Kodric-Brown and Brown 1984; Hill 2006; Clutton-Brock and McAuliffe 2009; Wacker et al. 2016; Tomkins et al. 2018).

Higher incidence of paternal care and monogamy (particularly among birds) compared to other taxa may also magnify selective behavior by increasing the stakes of finding a suitable mate (Unger and Sargent 1988; Searcy 1992; Black and Hulme 1996; Kraak and Weissing 1996; Gozlan et al. 2014). Conversely, the intense competition between males in polygynous systems has spawned a paradigm that intrasexual competition drives sexual selection more than intersexual selection in such systems (McEachern et al. 2009). Despite this, several examples of female mate choice have been observed in mammals; notably in ungulates such as red deer *Cervus elaphus* (McComb 1991; Charlton et al. 2007), elk *Cervus canadensis* (Kie et al. 2013), fallow deer *Dama dama* (Clutton-Brock and McComb 1993), Rocky Mountain bighorn sheep *Ovis canadensis* (Hogg 1987), and reindeer/ caribou *Rangifer tarandus* (Røed et al. 2005; Djakovic 2012). A persistent caveat among studies of female mate choice in ungulates is the difficulty in delineating the relative influences of intra- and inter-sexual selection (Clutton-Brock and McAuliffe 2009). Indeed, competition between males often results in selection for larger body size and weaponry that males may use to constrain female choice, which may complicate such distinctions (Clutton-Brock and McAuliffe 2009).

Despite this, female mammals invest highly in their (often altricial) offspring and are thus expected to exhibit a high degree of choosiness regarding potential mates (Trivers 1972).

Reindeer provide an excellent opportunity to examine female choice in a polygynous system. Notably, reindeer exhibit strong breeding phenology, where calving season is synchronized with green-up in Arctic and boreal ecosystems (Mallory and Boyce 2018; Paoli et al. 2020). Calving times, and by extension breeding times, are thus important factors in calf survival as neonates depend on the increased abundance of food at green-up to achieve good body condition before the coming winter when mortality may exceed 50% (Eloranta and Nieminen 1986; Crête and Huot 1993; Weladji and Holand 2003; Mahoney et al. 2016; Mallory and Boyce 2018). Given the likelihood of high mortality in neonates, it is expected that natural selection will favor larger calves as size is associated with body condition and decreased mortality. Females are thus expected to preferentially mate with males that may impart large size to their offspring, thereby affording the calf a head start (Bro-Jørgenson 2011; Djakovic 2012).

Reindeer mating systems are characterized by female defense polygyny, in which males compete to monopolize access to receptive females (Bergerud 1974; Hirotani 1994; Holand et al. 2004; Røed et al. 2005). As such, male reindeer establish a hierarchical system, where rank appears to be related to an individual's age, body size, and the size and complexity of antlers (Hirotani 1994; McElligott et al. 2001; Røed et al. 2005). Dominance hierarchies are evident in the formation of mating groups comprised of a single dominant male, 1 or more females, and often 1 to several satellite males who remain on the periphery (Bergerud 1974; Hirotani 1994). Within these groups, the dominant male has been shown to secure the most copulations by prohibiting access to females through agonistic interactions with other males (Bergerud 1974; Hirotani 1994). Moreover, females have been observed to prefer mating with dominant males, with a tendency to avoid sub-dominant individuals (Djakovic 2012).

Despite this observed preference for high-ranking males, sub-dominant males frequently secure copulations; occasionally even gaining more paternities than some older, larger males (Røed et al. 2005). This may be the result of several interacting factors. In populations with relatively even sex ratios, dominant individuals may have difficulty fending off advances by numerous satellite males due to increased competition (Reale et al. 1996; Clutton-Brock et al. 1997). Mating group size and stability may also influence sub-dominant male access to females (L'Italien et al. 2012). Critically, reindeer do not appear to tend females after copulation, possibly allowing subsequent copulation attempts by rival males if the female is still receptive (Bergerud 1974). Indeed, subsequent copulations may be likely if a female remains receptive (i.e. following an unsuccessful attempt) as females often travel between groups while foraging (Djakovic 2012).

Multiple mating may provide an avenue for cryptic female choice in reindeer, which may explain the success of sub-dominant males. Multiple mating has been described in several mammalian species (Wolff and Macdonald 2004), including several that are generally considered polygynous (McEachern et al. 2009). Multiple mating among female ungulates has been described in white-tailed deer *Odocoileus virginianus* (DeYoung et al. 2002; Sorin 2004) and Soay sheep *Ovis aries* (Wolff and Macdonald 2004), but no such research has been acknowledged in reindeer. This may be due to difficulties in observing multiple copulations by a single female in the field, as reindeer courtship displays may last several hours. Additionally, female mating strategies may not be as conspicuous as male strategies in polygynous systems. Detecting multiple mating by instances of multiple paternity in calves is likewise difficult because female reindeer typically give birth to a single calf during the calving season, and twins are very rare. Despite this, anecdotal observations of multiple mating in the field (personal observations) raise questions of how frequently such behavior occurs in natural populations.

Knowledge of the extent of multiple mating (essentially an example of polyandry) in reindeer is important for the broader characterization of their mating system. Distinction between pure polygyny (males monopolize several females, while females mate with a single male) and polygynandry (both sexes mate with multiple partners) is necessary as the 2 systems may have different consequences regarding population genetics (McEachern et al. 2009). Indeed, polyandry is associated with increased sexual conflict, which may elevate the fitness costs of reproductive behaviors (Holmand and Kokko 2013). Polygyny may also increase genetic relatedness within groups, while reducing the effective population size when compared to promiscuous or polygynandrous systems (McEachern et al. 2009).

We examine the capacity for active mate choice in female reindeer by addressing the role of multiple mating in this assumed polygynous system. Our objectives are to first, determine whether multiple mating is a common strategy among female reindeer by measuring the frequency of its occurrence in a semi-domesticated population. Second, to assess whether multiple mating is an active strategy (female choice) or a passive reaction to sexual harassment by sub-dominant males. We will achieve this by examining the occurrence of mismatch between the identity of males observed copulating with a female, and the identity of the male who secures the paternity of the female's calf. To do this, we combined behavioral and genetic data collected during seven rutting periods from a semi-domesticated herd in Kaamanen, Finland.

Materials and Methods

Study area and population

We conducted the study at the Kutuharju Reindeer Research Station in Kaamanen, Finland (69°N, 27°E) using a semi-domestic herd of approximately 100 individuals. The study area was composed of several large enclosures characterized by stands of white birch *Betula papyrifera* and Scots pine *Pinus sylvestris* with lakes and boggy areas interspersed throughout. The reindeer were kept in 1 of 2 enclosures (Lauluvarra = 13.8 km², Sinioaivi = 15.0 km²) during the rut, and could roam and associate freely. The age structure and sex ratio were manipulated each year as part of a larger project that has been ongoing since 1996. Males were fitted with a VHF radio collar displaying a unique number, which was associated with an identifying code allowing them to be tracked and identified in the field. Females were fitted with collars displaying a unique number-color combination.

Data collection

Data for this study was collected in accordance with existing methodology (described below) that has been used for the long-term study of this herd (Roed et al. 2005; L'Italien et al. 2012; Tennenhouse et al. 2012; Weladji et al. 2017;

Paoli et al. 2020). Data for this herd exists from 1996 onward; however, we limited our analyses to 7 years: 2001, 2003, 2004, 2005, 2006, 2007, and 2010. Excluded years were left out of our analyses due to an absence of important measurement data resulting from focus on ongoing experiments that superseded regular data collection protocol. Herd age structure and sex ratio varied across years resulting from manipulative experiments conducted throughout the duration of study (Table 1).

Sampling was conducted over an approximately 2-week period (between late September and mid October depending on the year) beginning during the pre-rut and continuing into the early post-rut. As the exact rutting dates change yearly in accordance with environmental variation, we maintained constant communication with reindeer herders at the research station to ensure the 2 weeks period encompassing the rut was sampled each year. We tracked reindeer via radio telemetry using radio collars on each male in the herd to find mating groups. Males were tracked instead of females because mating groups congregate around males and are dynamic, with females leaving and joining new groups regularly. Upon finding animals, we recorded the size and composition of mating groups, as well as any changes to the group structure or composition during observation. We recorded the rutting behavior of male and female reindeer using a 15-min focal observation technique. Using this technique, each male and female in a mating group was observed for 15 mins, during which activity was classified into one of the following categories at 15-s intervals: rest, stand, walk, eat, fight, chase male, chased by male, chased by female, herd, spar, displace male, displace female, displaced by male, displaced by female, court, follow, flehmen, attempt copulation, or successful copulation (i.e. penetration lasting a couple of seconds and copulated female displaying immediate visible hind legs cramps), along with the identity of all individuals involved in interactions. These focal observations were supplemented with ad-libitum observation averaging about an hour per mating group and extending to several hours in mating groups where a copulation attempt was imminent. In such cases the animals were observed until a successful copulation was deemed to have occurred (which took several hours in some cases due to length of courtship displays). Behavioral observation occurred from dawn to dusk each day, ceasing when darkness precluded accurate observation. During the following calving season, females were herded into a calving enclosure where we weighed, sexed, and collected a blood sample from each newborn calf for subsequent paternity analysis in lab. The calving enclosure was surveyed daily during the calving season, so a precise date of birth is known for each animal. Adults were similarly herded into a funneled weighing enclosure where they were weighed prior to the rut.

Paternity analysis

Following methodology common to previous analyses on paternity in this herd (Røed et al. 2002), we determined the paternity of all newborn calves using 15 reindeer specific microsatellite loci DNA markers from blood samples obtained from sexually mature males and all newborn calves. The results of the paternity analyses were expressed as either a match or a mismatch. A match occurred when the male observed copulating a female was genetically confirmed to be the sire of her calf. Conversely, a mismatch occurred when the male observed copulating a female was confirmed not to be the sire of her calf (i.e. a different male was confirmed to be the sire).

We assessed the frequency of multiple mating using match/mismatch as a proxy. Using this metric, we could confirm that multiple mating had occurred by showing that an additional male had copulated the same female. Instances of multiple mating may also be observed in the field, as we observed several females mating with multiple males. However, using match/mismatch allowed us to detect multiple mating even in cases when a second copulating male could not be observed (i.e. if we only saw a female with 1 male, we would still know she had mated with more if the observed male did not match the results of the paternity test).

Statistical analyses

To test whether multiple mating was related to harassment by sub-dominant males, we used multiple logistic regression to determine whether females were more likely to mate with additional males in years with higher percentages of males. Our model contained terms representing the effects of male body mass, percentage of the herd comprised of males (hereafter referred to as 'sex ratio'), and the variance in male body mass for each year. We calculated the variance in body mass between males in all years and included this as a parameter to validate the assumption that female reindeer can differentiate between males of similar size. We included the genetic ID of both males and females as random terms in our model to account for repeated measurements of a single individual within or across years. Under the assumption that it is

Table 1. Variation in sex ratio (percent of herd that are male) and age structure of the semi-domestic reindeer population in Kaamanen, Finland during the years 2001, 2003, 2004, 2005, 2006, 2007, and 2010. Two male age structures are used: Young (only males of 1–1.5 years) and Mixed (young and older males together)

Year	Male percent	Age structure	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Total males	Herd size
2001	12	Young	11	0	0	0	0	0	11	92
2003	7	Mixed	1	1	2	0	0	0	4	57
2004	12	Mixed	4	2	1	4	0	0	11	92
2005	30	Mixed	12	4	1	0	2	0	19	63
2006	26	Mixed	7	5	4	2	0	0	18	69
2007	22	Mixed	9	6	3	2	2	1	23	105
2010	24	Mixed	4	4	4	5	1	1	19	79

more difficult for males to monopolize females when there are many competitors, we would expect to see an increase in multiple mating at higher male percent composition. We ran the logistic regression model twice; once with the response variable expressed as a binomial value (match/mismatch) and once with the response expressed as a ratio of successes (match) over attempts (hereafter referred to as the 'conversion rate' of copulations into paternities). This addressed a possible issue arising from the expectation that larger males would have many more copulation attempts and thus the statistical weight for mismatch would be higher in small males. Both models produced similar results; however, the model using the response expressed as successes over attempts was used because of greater model convergence.

In all cases, male body mass was converted to relative body mass to account for the amalgamation of data across all years. We did this by dividing the mass of each male within a year by the mass of the largest male within the same year. By doing this, each male's body mass was expressed as a proportion of that of the largest male in each year (who was assigned a body mass value of 1). Yearly variation in herd composition and individual body masses potentially introduces the problem that a large male in 1 year may be considered smaller than average in another year. This may skew results towards smaller individuals if the largest male in a year with only small competitors secures the most paternities. By standardizing male body mass, we circumvent this issue without compromising statistical power by treating each year separately. Another potential solution was to control for yearly variation by including year as a variable within our model. However, since year was highly correlated with 2 variables of interest, male body mass and sex ratio, this was deemed inappropriate.

We further analyzed the validity of multiple male mating as active strategy through investigation into whether it conferred an observable fitness benefit to calves. To do this, we used a 3-way GLM to determine whether polyandrous females gave birth to larger calves. The primary explanatory variable was binomial and denoted whether a female had mated with a single or multiple males. Our model also included female weight, to account for the fact that a calf's weight is expected to reflect the size of their mother. Calf weight was used as the response variable as weight is thought to reflect body condition, which is associated with decreased mortality (Mahoney et al. 1990, 2016).

All statistical analyses were conducted using the program R (R Core Team 2018).

Results

Frequency of multiple mating

A total of 117 copulations were observed over the 7 years sampled during this study. Of these, 65 resulted in paternity match, leaving 52 cases of mismatch across all years (44.4%). A total of 97 females were sampled, 41 of which (42.3%) were observed or inferred to have mated with more than 1 male during the same rutting season. By "inferred" we mean females that were seen to mate with 1 male but conceived a calf from a different male. The proportion of females who mated with multiple males during a single year ranged from 0% (2006 and 2010) to 60% (2001 and 2007) (Figure 1). However, only 4 and 5 copulations were observed in 2006 and 2010, respectively (Figure 1). For years where multiple mating was observed, an average of 47.4% of females mated with more than 1 male.

Factors driving multiple mating

The herd sex ratio differed significantly between years (ANOVA; $F = 22.951$, $df = 1$, $P < 0.001$), ranging from 7% male in 2003 to 30% male in 2005 and averaging 19% across years (Table 1). Male mass likewise varied significantly across years (GLM; $F = 57.799$, $df = 1$, $P < 0.001$), with the largest
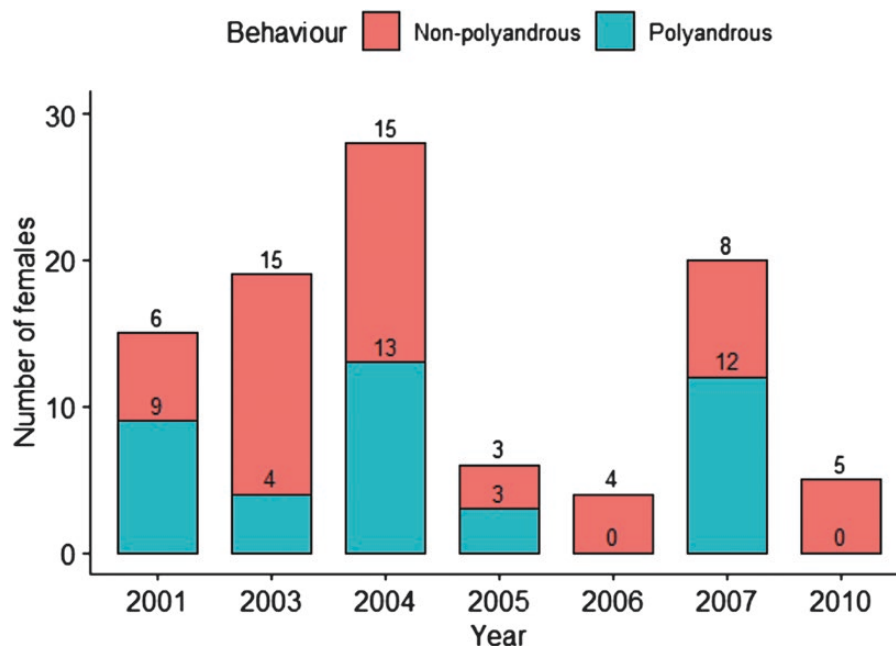
Figure 1. Number of observed polyandrous and non-polyandrous female reindeer observed during the 2001, 2003, 2004, 2005, 2006, 2007, and 2010 rutting seasons. Numbers within the coloured bars indicate the number of females observed exhibiting each behavior, which add up to the total number of copulations recorded in each year (See online version for color figure).

copulating male observed weighing 172 kg (2007) and the smallest weighing 70 kg (2001). Neither herd sex ratio (P = 0.092; Table 2) nor variance in male size (P = 0.183; Table 2) significantly predicted the conversion rate of copulations to paternities for males across years. Conversion rate varied significantly according to male size (P = 0.013; Table 2), with smaller males more likely to experience mismatch than larger males (Figure 2).

Only female weight was observed to significantly predict calf weight (P = 0.002; Table 3). Neither status (mated with multiple males or mated with a single male) nor its interaction with female weight significantly predicted calf weight (all P > 0.05; Table 3).

Discussion

Our results suggest that multiple mating is a common rutting behavior among female reindeer. We observed that 42.3% of females exhibited multiple mating over our 7-year study, with as many as 60% of females mating with multiple males during certain years. Moreover, these are conservative estimates of the extent of multiple mating given that logistical restrictions prevent us from recording all instances where multiple mating occurs. Indeed, observations span only a 2-week period and observers are too few to effectively sample all males simultaneously. Resultantly, there are likely cases where females copulate with additional males, but no observers are present to record (Supplementary Table S1). This is reflected in the occurrence of mismatch where

Table 2. Results of the logistic regression assessing the influence of male percent composition, relative male body mass, and variance in male mass on conversion rate (of copulations into paternities) among male reindeer in Kaamanen, Finland during the years 2001, 2003, 2004, 2005, 2006, 2007, and 2010

Model	Estimate	SE	z value	P value
Relative body mass	0.10778	0.04330	2.489	0.0128
Percent male	0.11457	0.06806	1.683	0.0923
Mass variance	–0.08719	0.06552	–1.331	0.1833
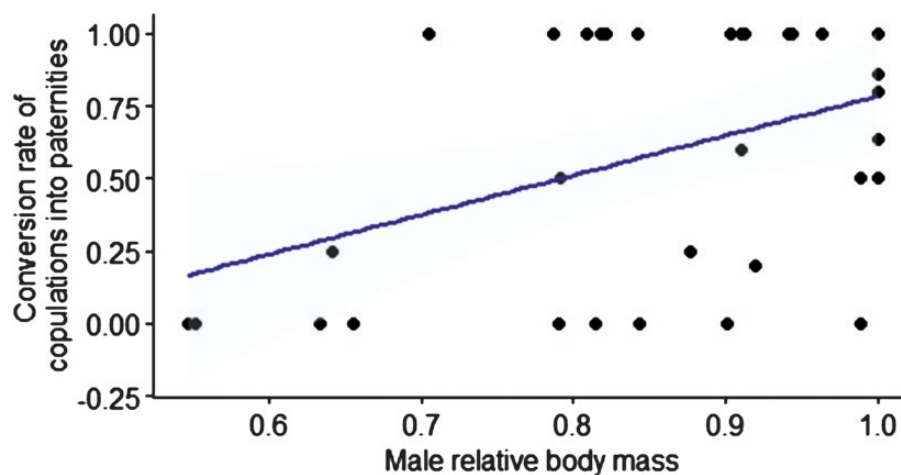
we did not observe the copulation that resulted in paternity (Supplementary Table S2). Also excluded are instances where multiple mating may occur despite the confirmed sire of a female's calf being the only male observed copulating her. In such cases, the occurrence of match does not necessarily preclude multiple mating, however, the occurrence of mismatch irrefutably indicates that multiple mating has occurred.

Findings that match rate is uninfluenced by the herd sex ratio support a view that multiple mating is an active reproductive strategy and not simply a response to sexual harassment by competing sub-dominant males. If multiple mating is primarily driven by male harassment, we would expect increased instance of multiple mating at higher male percent composition. An increased sex ratio should increase the opportunity for harassment by increasing the number of potential harassing males per female, and possibly by providing an environment that favors male targeting of specific females (Uccheddu et al. 2015). Indeed, previous studies have indicated that greater percentage of males limits the ability of high-ranking males to effectively monopolize females by increasing intraspecific competition (Reale et al. 1996; Clutton-Brock et al. 1997). Such competition should increase the frequency of harassment, which should result in a significant correlation between match and the percent of the herd that is male. It is also possible that the decreased capacity of dominant individuals to constrain female choice in populations with higher percentages of male may promote active choice. However, in this case we would expect less multiple mating in favour of females mating with a single preferred male. Moreover, copulations by satellite males are typically done sneakily or by force and may involve active avoidance by females (Bergerud 1974). Female preference for dominant individuals thus likely does not result solely from male constraint of choice. Findings that calves of females with several mates do not differ significantly in size to those of single mate females also challenge the notion of active female choice. Active choice suggests that there is some benefit in choosing 1 strategy over the other, which is not immediately evident. However, fitness benefits for calves may manifest in ways other than birth weight.

Figure 2. The influence of male relative body mass on the conversion rate of copulations into paternities among males during the 2001, 2003, 2004, 2005, 2006, 2007, and 2010 rutting seasons. The blue line shows the regression model predictions, and the gray area represents the 95% confidence interval (See online version for color figure).

Table 3. Results of the two-way GLM assessing the influence of multiple mating and female weight on body condition among 91 reindeer calves born in Kaamanen, Finland during the years 2001, 2003, 2004, 2005, 2006, 2007, and 2010

Model	Estimate	SE	t value	P value
Status (polyandrous or not)	7.62728	18.23275	0.418	0.67674
Female weight	0.40558	0.12376	3.277	0.00151
Status × Female weight	–0.07613	0.21825	–0.349	0.72807

Our results reinforce sentiments proposed by previous studies favoring genetic estimators over behavioral estimators of paternity (Coltman et al. 1999). Mismatch not only indicates multiple mating, but also directly measures the frequency of error associated with estimating male reproductive success without genetic confirmation. A 44.4% mismatch rate effectively translates to a 44.4% chance of misattributing paternity. Critically, the short duration of copulation makes it difficult to confirm that a successful penetration will lead to fertilization, meaning some observed copulations may still be unsuccessful. This has important consequences for the estimation of life-history and population parameters, many of which use reproductive success as an important coefficient (McEachern et al. 2009). Assurance that estimates of reproductive success are accurate are therefore crucial regarding the management and conservation of both wild and domestic populations.

To our knowledge, multiple mating has yet to be recognized and considered as a persistent part of female rutting behavior. This is strange because multiple mating is common in many ungulates (DeYoung et al. 2002; Sorin 2004; Wolff and Macdonald 2004). Moreover, reindeer mating systems appear to be conducive to multiple mating. Male reindeer, unlike other male ungulates, do not tend females after copulating (Bergerud 1974; Holand et al. 2012), allowing subsequent attempts to be made by other males. Moreover, female reindeer are polyestrous during the rut and may remain receptive following copulation if fertilization has not occurred (McEwan and Whitehead 1972). Like other female ungulates, reindeer invest heavily in their offspring and are thus expected to prefer males that will impart good fitness to their calf. Multiple mating, in essence, dilutes each male's chance at gaining paternity.

Of all variables tested, only male weight significantly predicted the likelihood of match. Match rates tended to increase with increasing male weight, suggesting that smaller males are more likely to incur reduced reproductive success resulting from multiple mating by females. Furthermore, these results suggest that female preference for large body size in males may extend beyond mate acquisition. Previous studies on reindeer have found that reproductive success in males is highly correlated with dominance rank, which itself is correlated with age, body size, and antler complexity (Kodric-Brown and Brown 1984; Hirotani 1994; McElligott et al. 2001; Røed et al. 2005). However, these studies do not consider multiple mating and assume that these preferences are expressed solely in a female's choice of who to mate with. Our results support a preference for large body size but may also suggest that this preference may not solely manifest itself in a priority of access model. As pointed out by Kekalainen and Evans (2018), what happens after copulation is more complicated than previously thought. Indeed, in the context of multiple mating, preference for larger males may mean that either their sperms are more competitive, and that female are able to discriminate in their favor, or that this is chance resulting from them having a higher number of mating opportunities, including with females that mated already with subordinates. In these situations, the observed results may approximate a fair lottery as has been reported in bighorn sheep, resulting from "retaliatory" copulations (Hogg, 1984, 1988; Hogg and Forbes 1997). Based on our own experience, "retaliatory" copulations are unlikely in reindeer. Indeed, we have seen repeated times the same male copulating more than once with the same female but have not witnessed acts of retaliation per se following copulation by subordinates. This may not contradict the fact that dominant males may constrain female choice.

As previously mentioned, our results preclude a sexual harassment hypothesis for the occurrence of multiple mating in female reindeer. The fact that large males are less negatively influenced by multiple mating than small males despite undergoing presumably similar dilutive effects suggests that polyandry is an active female strategy. In other polygynous systems, multiple mating has been associated with defense against infanticide by unrelated males (Wolff and Macdonald 2004). However, given that infanticide is uncommon in reindeer, this is an unlikely explanation for multiple mating in females. Here we suggest 2 competing hypotheses for multiple mating in reindeer: 1) the guard against male infertility hypothesis and 2) cryptic post-copulatory selection (Wolff and Macdonald 2004).

The guard against male infertility posits that females may mate with multiple males to ensure pregnancy in the event that the first copulation is unsuccessful (Wolff and Macdonald 2004). This has been observed in other mammals where few individuals gain the majority of reproductive success (Soay sheep; Preston et al. 2001; Agile antechinus *Antechinus agilis*; Kraaijeveld-Smit et al. 2002). Several studies on reindeer reproductive success have found that, despite some variation, a few high-ranking males gain most of the paternities during a single rut (Hirotani 1994; Røed et al. 2005). These high-ranking males expend a lot of energy during the early and peak rut, typically ceasing foraging activity to focus on establishing mating groups and guarding receptive females (Bergerud 1974; Hirotani 1994). It is possible that high-ranking males become exhausted, or even deplete their sperm in the peak rut leading to increased infertility during the late rut (Preston et al. 2001). Notably, high-ranking males have been observed to decrease reproductive effort during the late rut, while lower-ranking males increase their reproductive success by maintaining the same effort (Tennenhouse et al. 2012). Multiple mating may thus compensate for the increased risk of copulating with an exhausted male. If this were true, we would expect greater success (match rates) in later copulating individuals. Additional analyses examining multiple mating may benefit from separating the rut into pre-rut, peak-rut, and late-rut periods, which would give a better idea as to how this behavior changes over the course of the rutting season. Naturally, most copulations with near-exhausted males may be successful, with subsequent copulations being made for insurance only. This assumes that it is preferable to conceive a calf with a low-quality sire than it is to not reproduce during a given year, which may be true as the fertility rate in this herd is typically over 80% (Eloranta and Nieminen 1986).

Likewise, establishing which estrous period copulations occur in is critical as the interpretation of multiple mating may change substantially depending on whether it occurs within the same estrous period. Indeed, increased copulations in later estrous periods may suggest a rescue mechanism while multiple mating in the first estrous period may indicate a cryptic selection strategy.

Active multiple mating may also indicate a capacity for post-copulatory selection in reindeer. Post-copulatory selection in mammals is usually facilitated by some sort of reproductive delay (Orr and Zuk 2014). The importance of phenology in reindeer mating systems calls into question the feasibility of such delays. Studies on reproductive delay in reindeer are few, but generally agree that delayed implantation is unlikely (Retzius 1900; Ringberg and Aakwaag 1982). Indeed, delayed fertilization between estrous periods could potentially facilitate sperm competition between males. Notably, larger male reindeer are expected to have higher sperm counts than smaller males and thus would be expected to outperform smaller males in competitions between sperm (Møller 1989). This may offer some explanation as to why larger males tend to copulate more successfully across all years.

We observed a high degree of multiple mating in this reindeer population, indicative of an adaptive mating strategy rather than a passive reaction driven by male rutting behavior. No clear conclusions could be drawn regarding the drivers of multiple mating except that female preference for large males persisted despite many females copulating with males of varying sizes. Our results justify further investigation into dominant male infertility and cryptic post-copulatory selection as explanations for multiple mating in female reindeer. Analysis of the capacity for delayed fertilization, in addition to examination of sperm quality differences among males, would be a good starting point for further inquiry into potential physiological mechanisms for sexual selection in female reindeer. Moreover, inquiry into the fitness consequences of multiple mating may shed light on why some females adopt this strategy.

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Conflict of Interest

The authors have no competing interests to declare.

Ethics Statement

The data collection and safe handling of animals was conducted in accordance with the Animal Ethics and Care certificate provided by Concordia University (Protocol number 30000303) and by the Animal Experiment Board in Finland (Protocol number ESAVI/7711/04.10.07/2016).

Authors' Contributions

R.B.W. and Ø.H. conceived the ideas; R.B.W, Ø.H, K.H.R. collected the data. K.H.R. conducted paternity analyses. K.R.C. and R.B.W. performed the statistical analyses. K.R.C drafted the manuscript that was edited by R.B.W, Ø.H. and K.H.R.

Data Availability

Will be made available on request.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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