Mismatch between calf paternity and observed copulations between male and female reindeer (*Rangifer tarandus*): are female reindeer polyandrous?

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ABSTRACT

Mismatch between calf paternity and observed copulations between male and female reindeer (*Rangifer tarandus*): are female reindeer polyandrous?

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In polygynous systems, such as that exhibited by reindeer (*Rangifer tarandus*), mate choice can be difficult to disentangle from male intrasexual competition because male behaviour may constrain female choice. Polyandry may provide an avenue for female mate choice, though it is difficult to identify using behavioural 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 polyandry in reindeer using a genetic approach to determine the success of observed copulations in a semi-domesticated herd in Kaamanen, Finland. Behavioural and genetic data were synthesized with population characteristics over a seven-year period to test the hypothesis that, if present, polyandry in reindeer is driven by sexual harassment from sub-dominant males. Finally, we test for prevailing patterns in the mating order of females to address the feasibility of polyandry as a mechanism for defense against male infertility or post-copulatory selection. We observed polyandry in 42% of females, with as many as 60% exhibiting polyandry in certain years. We found no evidence that polyandry resulted from sexual harassment by sub-dominant males, suggesting that it is likely a deliberate strategy among females. Female preference for larger males persisted despite polyandrous behaviour, however, we found no influence of male body mass on mating order, or of mating order on match/mismatch. Consequently, neither post-copulatory selection nor defense against infertility can be ruled out as a driver of polyandry among female reindeer.

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CONTRIBUTION OF AUTHORS

This research was originally conceived by Dr. Robert Weladji and Dr. Øystein Holand. Data came for this project came from a long-term dataset collected and managed by Dr. Robert Weladji and Dr. Øystein Holand. Dr. Knut Røed was responsible for conducting paternity analyses. As primary author, I was responsible for conducting all statistical analyses and for writing this thesis, with edits provided by Dr. Robert Weladji and Dr. Øystein Holand. I also contributed to this data set in the 2018 and 2019 field seasons, though these data were not used in this project.

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INTRODUCTION

Sexual selection, the process driving the evolution of adaptations that increase the

reproductive success of certain individuals over conspecifics of the same sex, arises primarily via

two mechanisms: intrasexual competition for access to mates, and intersexual competition, also

known as mate choice (Darwin, 1871; Jones and Ratterman, 2009). The interplay between these

two mechanisms gives rise to the various mating systems observed in sexually reproducing

animals (Clutton-Brock, 1989). 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, 2009). Females have, conversely, been considered a

limiting resource (Trivers, 1972; Clutton-Brock, 2009). Consequently, the bulk of research on

the reproductive ecology of polygynous species has traditionally addressed male behaviour.

More recently, an increasing body of literature has examined female mate choice. This shift in

emphasis may reflect a change in paradigm away from previous assumptions that male

intrasexual competition drives selection in polygynous systems.

Much existing literature on female mate choice has focused on birds and fish, likely

reflecting the conspicuousness of male reproductive displays among many species within these

taxa (Clutton-Brock, 2009). Birds are notable for their sexual dimorphism, with males in many

species developing elaborate ornamentation or colouration to attract the attention of females

(Hill, 2006). Likewise, female fish often prefer vividly coloured males (Wacker et al. 2016;

Tomkins et al. 2018) but may also select mates based on olfactory cues (Gozlan et al. 2014) or

size (Noonan, 1983). It is believed these characteristics function as honest indicators of fitness, and that females preferentially select mates on the basis that these phenotypic traits reflect a male's genetic quality (Kodrick-Brown and Brown, 1984; Hill, 2006; Clutton-Brock, 2009). However, a female's choice of mate may have consequences extending beyond the genetic viability of offspring (Searcy, 1992). For example, many male birds provide substantial paternal care to offspring, and may also secure territory for nesting (Searcy, 1992). Critically, many birds are monogamous and form lifelong pair bonds with mates (Black and Hulme, 2006). Choosing a suitable mate is therefore of great importance considering that mate choice directly influences important life history characteristics and monogamous females do not have the benefit finding a new mate during the next season (Searcy, 1992). Similarly, male fish may also provide paternal care (Unger and Sargent, 1988; Kraak and Weissing, 1996; Gozlan et al. 2014), and many studies have documented female preference for males whose nests already contain eggs (Unger and Sargent, 1988; Jamieson and Colgan, 1989; Kraak and Weissing, 1996). Contrastingly, most mammals are polygynous and rarely exhibit paternal care (Eisenberg, 1966).

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 (MacEachern et al. 2009). However, 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; Djackovic et al. 2012). A persistent caveat among studies of female mate choice in ungulates is the difficulty in delineating the relative influences of intra- and intersexual selection (Clutton-Brock, 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, 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 a unique opportunity to examine female choice in a polygynous system. Notably, reindeer exhibit extensive 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; Crete 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 favour calves that attain large body size quickly, and females will preferentially mate with males that impart large size to their offspring, thereby affording the calf a head start (Bro-Jorgenson, 2011; Djakovic, 2012). Predation risk may reinforce this preference by introducing further selective pressures for body size in calves, as attaining body size reduces vulnerability to certain predators (Mahoney et al. 1990; Mahoney et al. 2016).

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, 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; McEllington et al. 2001; Røed et al. 2005). Dominance hierarchies are evident in the formation of mating groups comprised of a single dominant male, one or more females,

and often one 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, while tending to avoid sub-dominant individuals (Djakovic, 2012).

Despite this observed preference for high-ranking males, sub-dominant males frequently secure copulations; occasionally even outperforming 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). When mating groups are large and unstable, females may be more difficult to herd and temporary harems may be formed by several competing males (Espmark, 1964). 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).

Polyandry may provide an avenue for cryptic female choice in reindeer, which may explain the success of sub-dominant males. Polyandry has been described in several mammalian species (Wolff and Macdonald, 2004), including several that are generally considered polygynous (McEachern et al. 2009). Polyandry among female ungulates has been described in white-tailed deer *Odocoileus virginianus* (De Young 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 polyandry 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 polyandry in the field (personal observations) raise questions of how frequently such behaviour occurs in natural populations.

Knowledge of the extent of polyandrous behaviour 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 two 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 behaviours (Holman 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). This has important consequences for population dynamics and viability as population genetic variation can influence fitness both at the individual and population levels (Lacy, 1997). This is particularly important considering the risks affecting wild populations, chief among which are concerns regarding high calf mortality (Mahoney et al. 2016). Moreover, the results of this study have important implications for sexual selection theory as they will help disentangle the influence of intrasexual selection from that of intersexual selection, which is more conspicuous and characteristic of polygynous mating systems.

In this study, we seek to determine the capacity for active mate choice in female reindeer by examining the role of polyandry in this assumed polygynous system. Our objectives are to first, determine whether polyandry is a common strategy among female reindeer by measuring the frequency of its occurrence in a semi-domesticated population. Second, to distinguish whether polyandry is an active strategy (female choice) or a passive reaction to sexual harassment by sub-dominant males. Finally, assuming affirmative results for the preceding objectives, we will examine whether polyandrous females exhibit a persistent pattern regarding which of their partners ultimately sires her offspring. We will test these hypotheses 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 will combine behavioural and genetic data collected during seven rutting periods from a semi-domesticated herd in Kaamanen, Finland.

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 one of two enclosures (Lauluvarra = 13.8 km^2, Sinioaivi = 15.0 km^2) 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. Animals were fitted with a VHF radio collar displaying a unique number-colour combination that allows them to be tracked and identified in the field.

Data collection

Data for this study was collected in accordance with existing methodology that has been used for the long-term study of this herd. Data for this herd exists from 1996 onward; however, we limited our analyses to seven years: 2001, 2003, 2004, 2005, 2006, 2007, and 2010. Excluded years were left out of our analyses due to an absence of important information and not as a result of sampling size. Herd age structure and sex ratio varied across years resulting from manipulative experiments conducted throughout the duration of study (Table 1)

Animals were tracked via radio telemetry. 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 behaviour of male and female reindeer using a 15-minute focal observation technique. Using this technique, males and females in a mating group

were observed for 15 minutes, during which activity is classified into one of the following categories at 15-second 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, along with the identity of all individuals involved in interactions. During the following calving season, we recorded birth weight and date for all newborn calves and collected a blood sample from each for subsequent paternity analysis in lab.

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 was confirmed to be the sire).

Statistical analyses

We assessed the frequency of polyandrous behaviour using match/mismatch as a proxy. Using this metric, we could irrefutably confirm that polyandry had occurred by showing that an additional male had copulated the same female. Instances of polyandry may also be observed in the field, as we observed several females mating with multiple males. However, using match/mismatch allowed us to detect polyandry even in cases when a second copulating male

could not be observed (i.e. if we only saw a female with one male, we would still know she had mated with more if the observed male did not match the results of the paternity test).

To test whether polyandry was related to harassment by sub-dominant males, we used multiple logistic regression to determine whether females were more likely be polyandrous in years with male-skewed sex ratios. 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. This ability was assumed to be necessary for meaningful choice in structuring mating order. 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 more difficult for males to monopolize females when there are many competitors, we would expect to see an increase in polyandrous behaviour 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 one 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 two variables of interest, male body mass and sex ratio, this was deemed inappropriate.

To assess whether polyandrous females patterned the order in which they copulated with potential sires based on size, we ran a Kruskal-Wallis test with mating order as the response variable and the relative mass of males as the explanatory variable. We then used logistic regression to determine whether the likelihood of match was influenced by the mating order. We included male relative body mass again in this model to test for size related patterns regarding which, of multiple males, won a paternity. Two competing assumptions were tested regarding mating order. First, that preference for size should persist, as size should be positively correlated with testes size in males (Ginsberg and Rubenstein, 1990). Increased testes size is associated with increased sperm production, larger number of sperm per ejaculate, and large sperm reserves, which should increase fertility (Møller, 1989). Second, that preference would be given to the first male in the mating order as they would have a 'head start' in terms of fertilization.

RESULTS

Frequency of polyandrous behaviour

A total of 117 copulations were observed over the seven 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 one male during the same rutting season. The proportion of polyandrous females during a single year ranged from 0% (2006 and 2010) to 60% (2001 and 2007) (Figure 1). However, only four and five copulations were observed in 2006 and 2010, respectively (Figure 1). For years where polyandry was observed, an average of 47.4% of females exhibited polyandry.

Factors driving polyandry

The herd sex ratio differed significantly between years (ANOVA; F=22.95, df=1, p<0.01), ranging from 4% male in 2010 to 30% male in 2005 and averaging 16.14% across years. Male mass likewise varied significantly across years (GLM; F=57.7, df=1, p<0.01), with the largest copulating male observed weighing 172kg (2007) and the smallest weighing 70kg (2001). Neither herd sex ratio (p=0.738, Figure 2) or variance in male size (SE=0.062, z=-0.833, p=0.405) significantly predicted the conversion rate of copulations to paternities for males across years (Table 2). Conversion rate differed significantly according to male size (SE=3.967, z=2.467, p=0.014; Table 2), with smaller males more likely to experience mismatch than larger males (Figure 3).

Influence of mating order

Across all years, we observed 41 polyandrous females. We know the identity and mating order of two or more mating partners for 34 of these females. Within this subgroup, females were observed copulating with an average of 2.2 partners during a single season; 29 females were observed with two partners, three were observed with three males, and two were observed with four males. Using this subset of 34 females, we examined relationships between male relative body mass and copulation order (Figure 4), and subsequently copulation order and match. We found no correlation between a male's relative body mass and their position within the mating order for a particular female (Kruskal-Wallis; chi-squared=14.995, df=16, p=0.525; Figure 4). Likewise, neither position within the mating order (SE=111.880, z=1.114, p=0.265) or male relative mass (SE=29.760, z=0.259, p=0.796) significantly influenced the likelihood of match within this subset. The largest male to copulate a particular female won the paternity in half of all cases and was the first to copulate the female in 19 cases (55.9%). However, there were only 9 instances (26.5%) where the largest male copulated a female first and also won the paternity.

DISCUSSION

Our results suggest that polyandry is a common rutting behaviour among female reindeer. We observed that 42.3% of females exhibited polyandrous behaviour over our seven-year study, with as many as 60% of females exhibiting polyandry during certain years. Moreover, these are conservative estimates of total polyandry given that logistical restrictions prevent us from recording all instances where polyandry occurs. Indeed, observations span only a two-week period and observers are too few to effectively sample all males simultaneously. Resultantly, there are likely many cases where females copulate with additional males, but no observers are present to record. This is reflected in the occurrence of mismatch where we did not observe the copulation that resulted in paternity. Also excluded are instances where polyandry 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 polyandrous behaviour, however, the occurrence of mismatch irrefutably indicates that polyandry has occurred.

Findings that match rate is uninfluenced by the herd sex ratio support a view that polyandry is an active reproductive strategy and not simply a response to sexual harassment by competing sub-dominant males. If polyandry is primarily driven by male harassment, we would expect increased polyandrous behaviour 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 favours male targeting of specific females (Uccheddu et al. 2015). Indeed, previous studies have indicated that male-skewed sex ratios limit 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 male-skewed populations may promote active choice. However, in this case we would expect less polyandrous behaviour 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.

Our results also reinforce sentiments proposed by previous studies favouring genetic estimators over behavioural estimators of paternity (Coltman et al. 1999). High rates of mismatch not only indicate polyandrous behaviour but also directly measure 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 penetration has occurred, meaning many observed copulations may 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, polyandry has yet to be investigated as a persistent part of female rutting behaviour. This is strange because polyandry is common in many ungulates (De Young et al. 2002; Sorin, 2004; Wolff and MacDonald, 2004). Moreover, reindeer mating systems appear to be conducive to polyandry. Male reindeer, unlike other male ungulates, do not tend females after copulating (Bergerud, 1974), 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). It is

possible that the perceived risk promiscuity poses to calf viability has resulted in its lack of

acknowledgement. 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. Polyandrous

behaviour, in essence, dilutes each male's chance at gaining paternity. This may be useful in

instances where a low-ranking male copulates a female first. In such cases, further copulation

attempts will dilute the chances of the inferior male gaining the paternity. However, we

observed that the largest male copulated polyandrous individuals first in over half of all cases

where a female mated with multiple males.

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 polyandry. 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 (Brown and Brown, 1984; Hirotani, 1994; McEllington et al. 2001; Røed et al.

2005). However, these studies do not consider polyandry 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 also suggest that this preference may not solely manifest itself in a priority of

access model. This is further supported by the apparent randomness in the mating order for a

particular female in relation to male body mass. If female mate choice functioned solely based

on allowing a preferred (large) male to copulate her, this bias should be reflected in the mating

order. Specifically, under the assumption that being the first to copulate a female is advantageous for fertilization, we would expect larger males to front the mating order most of the time.

Given the dilutive effect polyandry has on an individual male's chance to sire calves and the lack of evidence that this effect favours high ranking males, there must be another explanation for polyandry in reindeer. We tested the influence of position within the mating order on the likelihood of match (i.e. being the sire of a particular female's calf) and found no significant relationship. This may have resulted from the timing of copulations. As previously mentioned, females are polyestrous during the rut and associate more closely with males during estrous (McEwan and Whitehead, 1972). This allows them an additional chance to breed if they are not successfully fertilized during their first estrous period. The lack of correlation between mating order position and likelihood of match may reflect a mistiming of the initial copulation such that later copulating males have the advantage of copulating during the second estrous period. However, this explanation seems unlikely. In most cases, subsequent copulations occurred no more than a few days after the attempt by the first male. To have a significant advantage, subsequent copulations would need to occur two to three weeks following the initial attempt. Furthermore, male rutting behaviour reduces the chances of mistiming copulations with estrous cycles in females. Males typically remain in close consort with estrous females until both are satisfied that a successful copulation has occurred (Weladji, pers comm.). Moreover, males (particularly high-ranking males) may modify mating tactics to tend estrous ewes exclusively, reducing herding effort to instead focus on a high priority female (Weladji et al. 2017). Resultantly, we suggest it is unlikely mistimed copulations occur sufficiently frequently to significantly influence our results.

As previously mentioned, our results preclude a sexual harassment hypothesis for the existence of polyandry in female reindeer. The fact that large males are less negatively influenced by polyandry than small males despite undergoing presumably similar dilutive effects suggests that polyandry is an active female strategy. In other polygynous systems, multiple male 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 polyandrous behaviour in females. That said, the uncertainty introduced by polyandrous behaviour should carry significant risk, considering the perceived importance of mate choice to juvenile survival. It follows that polyandrous females should possess some capacity to ensure fertilization by the highest quality male, or otherwise that polyandry confers some tangible benefit to females. Here we suggest two competing hypotheses for polyandry in reindeer: 1) the guard against male infertility hypothesis, and 2) cryptic post-copulatory selection (Wolff and McDonald, 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 (Wolf and MacDonald, 2004). This has been observed in other mammals where few individuals gain the majority of reproductive success (Soay sheep; Preston and Stevenson, 2001; Agile antechinus *Antechinus agilis*; Kraaijeeveld-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. 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). Polyandry may thus compensate for the increased risk of copulating with a potential exhausted male. If this were true, we would expect greater success (match rates) in later copulating individuals. We did not observe skew towards males who copulated last in the mating order, however we did not address whether these copulations occurred immediately after the preceding attempt, or if they occurred during a later estrous cycle. Consequently, we cannot preclude guarding against infertility as a driver of promiscuity. Additional analyses examining promiscuity may benefit from separating the rut into pre-rut, peak-rut, and late-rut periods. This would give a better idea as to how polyandrous behaviour changes over the course of the rutting season. Moreover, it would provide a more accurate description of the frequency of promiscuity as female reproductive behaviour may vary throughout the breeding season (Tennenhouse et al. 2012). 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 percent (Eloranta and Nieminen, 1986).

Active polyandrous behaviour may indicate a capacity for post-copulatory selection in reindeer. Indeed, since females do not seem to dilute paternity solely to the detriment of (assumed) non-preferred males, it follows that they should have some means to select a preferred sire from a group of copulating males. This is supported by the fact that large males are less likely to 'lose' in cases of polyandry than smaller males. Curiously, although we saw increased conversion rates (increased matches relative to total attempts) among larger males in the full

data, this effect was not observed in our subset of females for which we could specify a chronological mating order. Paradoxically, this may also evoke cryptic post-copulatory selection if females simply allow sperm competition to decide which male wins the paternity of her calf.

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 Aakvaag, 1982). However, these studies only address delayed implantation, while other reproductive delays (i.e. delayed fertilization, delayed development) have received little attention. The occurrence of such reproductive delays in other mammals, including ungulates (Delayed fertilization; domestic sheep, domestic pig *Sus scrofa*, horse *Equus caballus*, ox *Bos taurus*; Birkhead and Møller, 1993) calls for further investigation into the capacity for similar delays in reindeer. Indeed, delayed fertilization between estrous periods could potentially facilitate sperm competition between males. This would also explain the observed independence of mating order regarding likelihood of match, otherwise the first male to inseminate a female should have a visible advantage. 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, though it does not explain why the same trend was not observed within the mating order for individual females.

We conclude that female reindeer exhibit polyandry during the rut. Our results indicate that at least 42.3% of all females sampled over our seven-year study mated with more than one male during a single season. This is a conservative metric for estimating polyandry as we can

only include observations we were present for. Females that were impregnated by the observed copulating male may still have mated with additional males when observers were not present. The high degree of polyandry we observed is indicative of an active mating strategy rather than a passive reaction driven by male rutting behaviour. This is supported by independence between match and the sex ratio (male percentage) of the herd. We found no evidence that polyandrous female reindeer deliberately structure their mating order to alter the outcome of paternity. No clear conclusions could be drawn regarding the drivers of polyandrous behaviour 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 polyandry 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 polyandry may shed light on why some females adopt this strategy. Finally, examination of the frequency of polyandry at different stages of the rut may help delineate the influence of male infertility on polyandry in reindeer.

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TABLES AND FIGURES

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

Year	Male percent	Age structure
2001	12	Young
2003	7	Mixed
2004	12	Mixed
2005	30	Mixed
2006	26	Mixed
2007	22	Mixed
2010	4	Mixed

Table 2. Results of the logistic regression models assessing the influence of the male percent composition on (a) conversion rate (of copulations into paternities), and (b) the influence of mating order on likelihood of match.

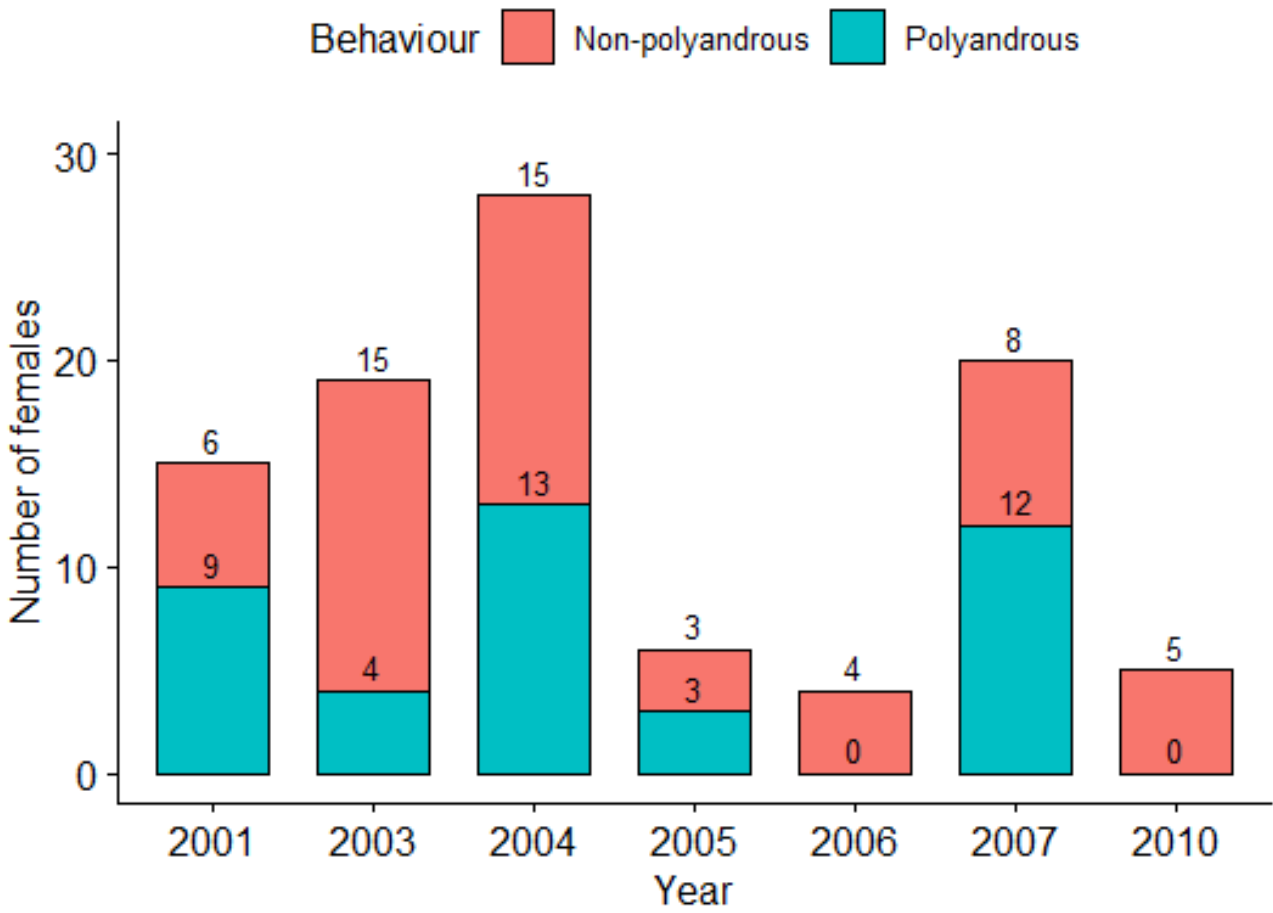| Model	Estimate	SE	z value	P value
(a) Conversion ~ percent				
Relative body mass	0.09788	0.03967	-2.027	0.0136
Percent male	0.02023	0.06057	2.467	0.7384
MassVariance	-0.05178	0.06213	0.334	0.4047
(b) Match ~ order				
Position in order	124.627	111.880	1.114	0.265
Relative body mass	7.703	29.760	0.259	0.796

Figure 1. Number of observed polyandrous and non-polyandrous female reindeer during the

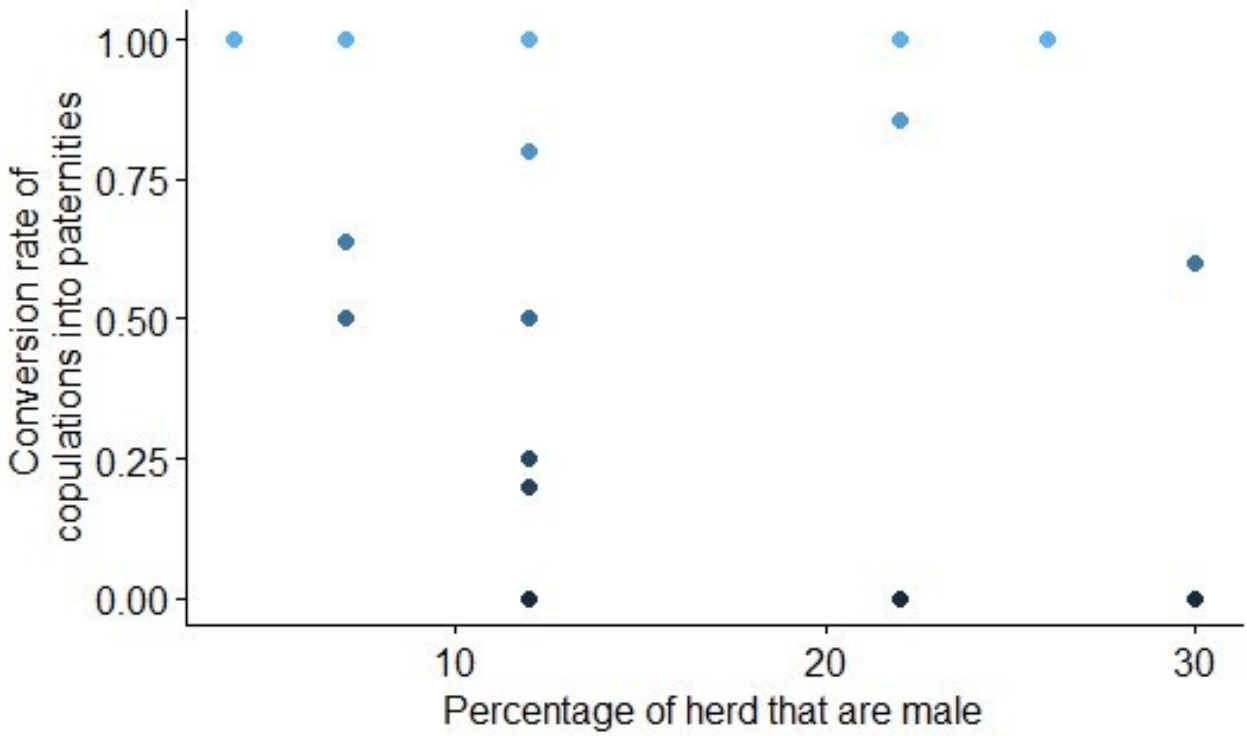2001, 2003, 2004, 2005, 2006, 2007, and 2010 rutting seasons.

Figure 2. Conversion rate of copulations among male reindeer during the 2001, 2003, 2004, 2005, 2006, 2007, and 2010 rutting seasons in relation to male percent composition (the percentage of the herd that is male). Darker points indicate lower conversion rates (suggesting more frequent polyandry).
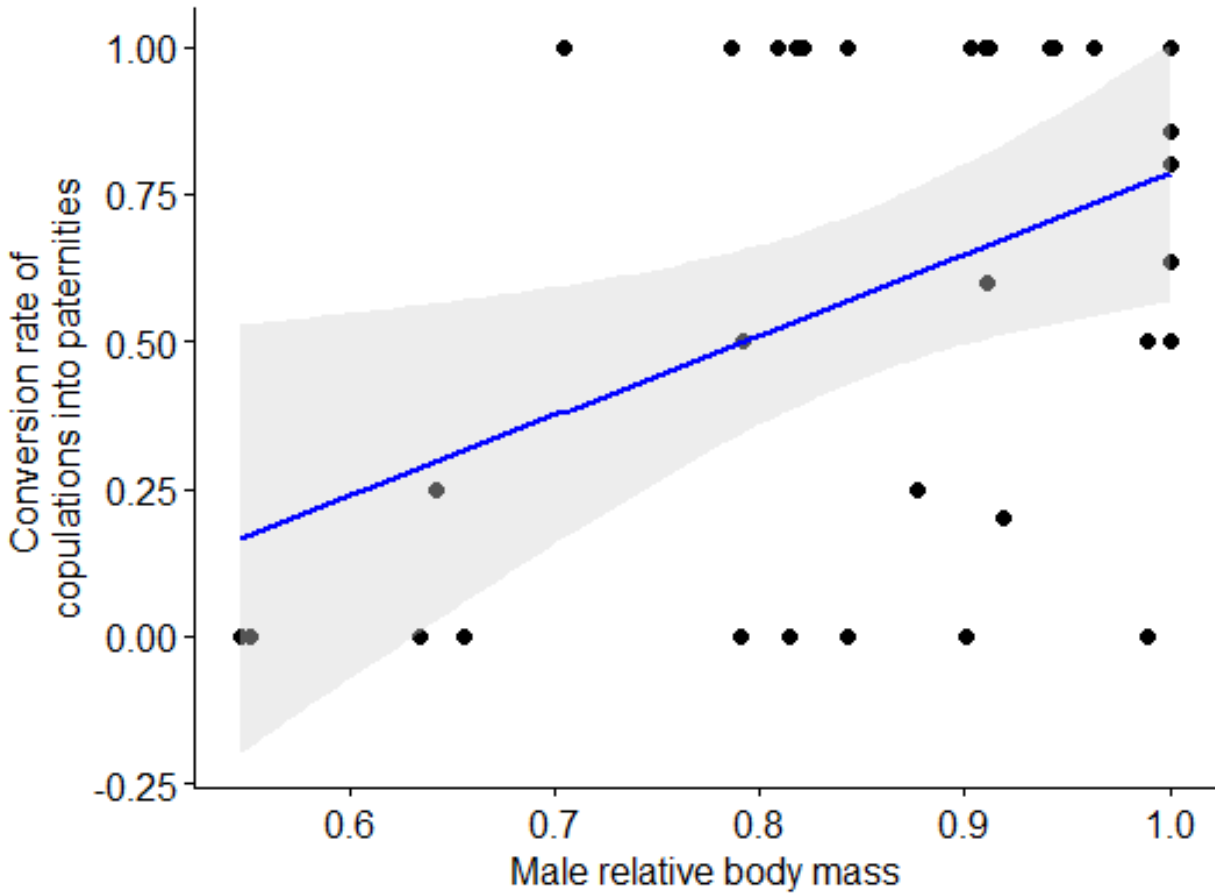
Figure 3. The influence of male relative body mass on the conversion rate of copulations into paternities among males during the 2001, 2003, 2004. 2005, 2006, 2007, and 2010 rutting seasons. The blue line shows the regression model predictions and the grey area represents the 95% confidence interval.
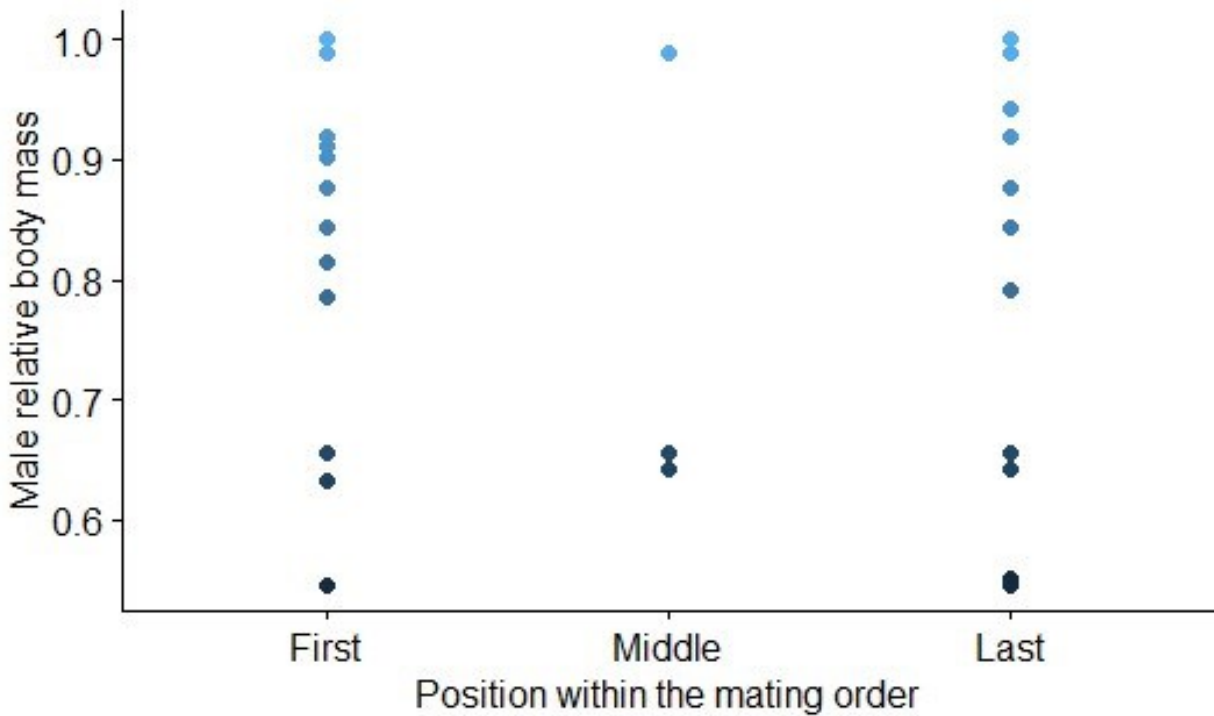
Figure 4. Male relative body mass in relation to position within the mating order for a particular female. The position 'middle' denotes all copulations between the first and last as there may be more than one middle value in cases where a female copulates with four or more males. Darker points indicate a lower relative body mass.