The influence of operational sex ratio on the mating behaviour of reindeer (*Rangifer tarandus* L.) during an experimental rut: the effect of male age

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ABSTRACT

The influence of operational sex ratio on the mating behaviour of reindeer (*Rangifer tarandus* L.)
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The operational sex ratio (OSR), the ratio of sexually active males to sexually receptive females, is one of the main measures used to predict the intensity and direction of mating competition, influencing the opportunity for sexual selection. Here we conducted the first experimental study to investigate how OSR and male age impacts the intensity of mating competition and the male activity budget in a large mammalian species, reindeer (*Rangifer tarandus*), under semi-natural conditions. We manipulated OSR on two levels in two enclosures, a female biased treatment (3♂:6♀ = OSR 0.5) and a sex balanced treatment (3♂:3♀ = OSR 1), over two years with males from two age groups (1.5 or 2.5-years-old), and with females of various ages. We found some support for prevailing OSR theory, notably with female intrasexual competition occurring at lower frequencies in OSR = 1. An emerging trend was noted for male intrasexual competition, with higher frequencies of occurrence in OSR = 1 for our 2.5-year-old males. Courtship behaviour was also found to occur at higher frequencies of occurrence among the 2.5-year-old males, however, there was no effect of OSR. Regarding the male activity budget, we found that 1.5-year-old males followed a more income breeding strategy, with no difference in foraging behaviour between OSR treatments. In contrast, our 2.5-year-old males had a significantly lower frequency of foraging behaviour in OSR = 1, presumably resulting from a higher occurrence of intrasexual competition. Vigilance behaviour was also found to occur at higher frequencies in OSR=1 for the 2.5-year-old males, likely due to females being more limiting. Our results suggest that age is an important factor with respect to how male reindeer respond to differing OSR values. Future research aiming to expand the generalizability of experimental OSR theory to a wider range of taxa and ecological conditions need to consider other factors that will impact competition for mates, such as prime reproductive age.

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CONTRIBUTION OF AUTHORS

The original conception for this thesis was developed by Dr. Robert Weladji. Guidance for the experimental design for both chapters was provided by Dr. Robert Weladji. I was responsible for the data collection over the course of two field seasons and the statistical analysis, with guidance by Dr. Robert Weladji for the statistical analysis of both chapters. As the first author, I was also responsible for the writing of both chapters of this thesis, with edits performed by Amélie Paoli, Dr. Robert Weladji, Dr. Holand Øystein, Dr. Jouko Kumpula, and Dr. Timo Soveri. Amélie Paoli also contributed with data collection.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Sexual selection is an evolutionary process that arises from variance in mating success, and results in the evolution of various morphological and behavioural traits among sexually reproducing organisms (Andersson and Iwasa 1996). The development of these secondary sexual traits is typically more pronounced in males; however, females do exhibit development of these traits, across various animal taxa as well (Kraaijeveld et al. 2007). Two main mechanisms of sexual selection are recognized, which include intrasexual selection and intersexual selection. Intrasexual selection refers to mating success being determined by within sex interactions, like male-male combat, whereas intersexual selection refers to mating success being determined by between sex interactions, such as mate choice.

The act of competing for mates can take various forms such as: scrambles, endurance rivalry, coercion, contests, mate choice, sperm competition and infanticide (Clutton-Brock and Parker 1995; Andersson and Iwasa 1996). The most common form of competition for mammalian species is likely contest competition (Andersson and Iwasa 1996). Contests comprise of various behaviours such as: fights, chases or threat displays between competitors; however, these behaviours vary greatly across species (Weir et al. 2011). The utilization of weaponry by animals in competition is common during contests, for example, antlers and horns in ungulates (Geist 1966; Barrette and Vandal 1986; Hoem et al. 2007), chilipeds in many decapods (Jachowski 1974; Barki et al. 1992), tusks in walruses (Sjare and Stirling 1996) and in frogs (Shine 1979).

Both reproduction and the various competitive behaviours associated with it can be an energetically expensive process. These associated energetic costs with reproduction are especially highlighted among polygynous species, such as ungulates, where the life history strategies differ between the sexes. The reproductive success of female ungulates largely depends on the successful rearing of her offspring, but the reproductive success of males depends on their ability to monopolize females during a short seasonal breeding period (Clutton-Brock, 1989). Most ungulate species are considered to utilize a capital breeding strategy to satisfy the energy requirements of reproduction, with males either completely stopping or drastically reducing their foraging behaviour during the breeding season (Jönsson 1997; Mysterud et al. 2005). Female ungulates typically engage in a mixed tactic encompassing both capital and income strategies due to the higher costs associated with gestation, lactation, and parental care after birth (Pond 1977; Gittleman and Thompson 1988).

Male ungulates have a relatively small window to reproduce successfully when a female is ready to conceive; however, gaining access to females is an energetically costly task, involving fighting with other males (Espmark 1964; McElligott et al. 1998), guarding territories (Alvarez 1993), and tending of females (Wolff 1998). The ability of males to successfully compete for females is influenced by secondary sexual traits, such as weapons and body size, both of which increase with age (Coltman et al. 2002; Preston et al. 2003a). These competitive behaviours can drain body resources, resulting in substantial weight loss, which has been observed in for example, fallow deer *Dama dama* (McElligott et al. 2003), moose *Alces alces* (Miquelle 1990), reindeer *Rangifer tarandus* (Mysterud et al. 2003), and red deer *Cervus elaphus* (Yoccoz et al. 2002). The somatic costs associated with engaging in rutting behaviours are thought to arise due to the tradeoff between engaging in maintenance behaviours or rutting behaviours, leaving the engaged individual more vulnerable to predation (Ydenberg and Dill 1986) and reducing their time devoted to foraging (Pelletier et al. 2009). These trade-offs result in their condition to decline as the mating season continues (Forsyth et al. 2005; Vannoni and McElligott 2009).

The various reproductive strategies utilized by both sexes to breed characterize the mating system exhibited by a species (Clutton-Brock 1989). Although different mating systems have long since been recognized, a consistent agreement regarding their classification has not been reached (Andersson and Iwasa 1996). One of the main classification criteria regards the number of mating partners per male and female. The four main broad categories when examining mating bonds are: monogamy (one male mates with one female), polygyny (a male will mate with multiple females), polyandry (a female will mate with multiple males), and promiscuity (males and females mate with multiple individuals; Krebs and Davies 1987). Among mammalian species, social monogamy and paternal care are relatively rare, such that 90% of all species exhibiting a form of polygyny (Eisenberg 1981; Clutton-Brock 1989).

Diverse forms of polygyny are exhibited across mammalian species, including: (1) Resource defense polygyny: when males indirectly control females by defending territories or resources from other males, (2) female-defense (harem) polygyny: when males directly defend aggregations of females by aggressively excluding other males (Emlen and Oring 1977; Clutton-Brock 1989), and (3) Leks: a relatively rare mating tactic, where females visit a communal male display area to mate (Ciuti and Apollonio 2016). For the evolution of polygamy (includes both polygyny and polyandry) in a species to occur, multiple mates or key resource that attract multiple mates must be defendable by individuals, which vary in their distribution both temporally and spatially (Emlen and Oring 1977).

Over the last five decades, there has been a significant amount of research investigating the ecological factors that promote differences in the intensity of sexual selection, both within and among species. While the intensity of sexual selection largely depends on the level of competition for mates, the degree of competition depends on two factors: the difference in parental investment of the two sexes and the operational sex ratio (Krebs and Davies 1987). Operational sex ratio (OSR) is considered one of the main predictors for the intensity and direction of mating competition (e.g., Kvarnemo and Ahnesjö 1996). The concept of operational sex ratio was first introduced by Emlen & Oring (1977), where it was described as the ratio of sexually active males to sexually receptive females, in a given breeding group, at a given time. When the OSR is biased towards one sex, it is expected that there will be more intense competition among members of the non-limiting sex for access to the limiting sex (Clutton-Brock and Parker 1992). Increases in intrasexual competition among members of the limited sex have been shown in many cases, such as in the sand goby *Pomatoschistus minutus* (Kvarnemo et al. 1995), guppies *Poecilia reticulata* (Jirotkul 1999), European lobster *Homarus gammarus* (Debuse et al. 1999), squinting bush brown *Bicyclus anynana* (Holveck et al. 2015), European bitterling *Rhodeus amarus* (Reichard et al. 2004) and Tibetan Macaques *Macaca thibetana* (Wang and Xia 2009).

Overall, across various taxa, most studies support the OSR based predictions for the occurrence of intrasexual competition among males (Emlen and Oring 1977;Weir et al. 2011; Janicke and Morrow 2018); however, it is less consistent when investigating male courtship behaviour. Traditional OSR theory predicts that male courtship rate will increase as the OSR becomes increasingly more male biased, however, many studies show the exact opposite trend (Verrell and Krenz 1998; Weir et al. 2011; Chuard et al. 2016). It has been suggested that this trend could simply be due to females being limited in supply within male biased OSR treatments; therefore, males will have less opportunity to engage in courtship displays (Jirotkul 1999; de Jong et al. 2012). Other studies have also investigated how OSR influences the use of alternative mating tactics by males. These studies have found that as OSR becomes increasingly more male biased, a shift from engaging in energetically costly fighting and courtship to less costly mating tactics like sneaking occurs (Grant et al. 1995; Mills and Reynolds 2003)

The intensity and direction of biases in OSR can be influenced by the potential reproductive rates (PRR) of the sexes (Clutton-Brock and Parker 1992), the spatial and temporal distribution of the sexes (Kruppa and Sih 1993), the adult sex ratio (ASR) of the population, differences between the sexes in age at maturity (Pitnick 1993), reproductive longevity, migration schedules, and mortality (Iwasa and Odendaal 1984). A major factor influencing OSR is the PRR, defined as the production of offspring per unit time each sex could achieve if they had unlimited access to mates, which often differs between the sexes. As this difference in PRR between the sexes increases, it is predicted that there will be intensified mating competition among the sex with the higher PRR (Clutton-Brock and Parker 1992). Thus, sexual differences in the PRR, commonly result in an OSR biased towards the faster reproducing sex.

Differences in PRR have been associated with differences in parental investment by the sexes in the form of gamete size. Females produce a few large macrogametes that are high in energy, whereas males produce many, highly mobile microgametes (Trivers 1972). Under conventional sex roles, parental investment is often much higher in females, attributed to their large energy investment in gamete production, nourishment of the embryo and care for the offspring. Consequently, many sexually active males will be searching for limited receptive females, leading to intrasexual competition among males for access to limited mates, allowing females to be choosy about whom they mate with (Andersson and Iwasa 1996).

Since the recognition of OSR being influenced by sex differences in PRR, there has been an emphasis in the literature on determining which sex is the most competitive in a species. This literature bias has resulted in there being less attention focused towards examining differences in intrasexual competition among both sexes, with respect to OSR (Grant and Foam 2002). Of the few studies that have investigated competitiveness of both sexes simultaneously, female biases in OSR have been found to also result in an increase in female-female competition (Kvarnemo et al. 1995; Debuse et al. 1999; Grant and Foam 2002; Forsgren et al. 2004).

Another important variable that has been suggested to influence mate competition is population density. Kokko and Rankin (2006), proposed that competition for mating opportunities would be correlated with density, where dominant individuals will have more opportunity to monopolize mates at higher population densities, thereby leading to an increase in the potential for sexual selection with density. Both population density and OSR are not independent of one another and together likely influence sexual selection by affecting the encounter rate of mates (Clutton-Brock and Parker 1992). Within the literature, there is contradictory evidence on the influence of density on competition intensity for mates. Some studies support the predicted increase in intrasexual competition with population density (Jirotkul 1999; Smith, 2007; Lauer, Sih and Krupa 1996), while others appear to oppose or show no clear support of these predictions (McLain 1992; Head, Lindholm and Brooks, 2008; de Jong et al. 2009).

To date, literature investigating the ability of OSR to predict the intensity and direction of mating competition have primarily dealt with males of small bodied taxa, in controlled environments (Weir et al. 2011). Various studies have suggested that the predictable effects of OSR may not be as generalizable across taxa as previously thought, proposing that the value of OSR will vary from species to species (Balshine-Earn 1996; Wacker et al. 2013; de Jong et al. 2009). Furthermore, very few studies have investigated how an experimentally manipulated OSR influences mating competition or the opportunity for sexual selection in mammalian species (but see: Zhang and Zhang 2003; Klemme, Ylönen and Eccard, 2007).

Reindeer (*Rangifer tarandus* L.) are an ideal species for studying mate competition. Firstly, males exhibit harem defense polygyny during a well-defined rutting period, where the gregariousness of females allows males to directly monopolize them (Espmark 1964; Skogland 1989; Geist 1999; Melnycky et al. 2013). Secondly, due to the lack of paternal care in this species, males are able to devote a considerable amount of energy towards reproduction, where they perform intensive fighting and courting behaviour (Espmark 1964; Skogland 1989). These dramatic competitive interactions between inidviduals result in considerable somatic costs during the rut (Mysterud et al. 2003; Holand et al. 2012). Thirdly, similar to other ungulate species, such as bighorn sheep *Ovis canadensis* (Hogg and Forbes 1997), Alpine ibex *Capra ibex ibex* (Willisch and Neuhaus 2009), mountain goats *Oreamnos americanus* (Mainguy et al. 2008) and feral goats *Capra hircus* (Saunders et al. 2005), reindeer exhibit age-dependent alternative mating tactics (Holand et al. 2012). The following male mating tactics are observed in reindeer: (1) Dominant: involves controlling a group through the use of agonistic interactions and tending of females, (2) Wannabe: includes prime males lingering around the group waiting for an opportunity to try and take control of the group through direct agonistic interactions with the dominant male, (3) Satellite: involves males hanging around the periphery of the group, waiting for an opportunity to take small female groups by isolating them from the main group, and (4) Sneaker: an age-dependent tactic, where young males sneak copulate females, since they are not able to maintain a group or tend females (Holand et al., 2012). Finally, since reindeer are a semi-domestic species and are maintained under semi-natural conditions, they provide an excellent opportunity to experimentally investigate the influence of OSR on reproductive behaviour of a mammalian species.

The aim of this thesis was to use an experimental approach to investigate how the rutting behaviour of 1.5 and 2.5-year-old male reindeer will be influenced when faced with either a balanced OSR (3♂:3♀) or a female-biased OSR (3♂:6♀), in an effort to expand the generalizability of present mating systems theory to an underrepresented taxon in the experimental OSR literature. Due to the rarity of studies in OSR literature investigating both male and female reproductive behaviour simultaneously, we will also incorporate female rutting behaviour in our design. Based on prevailing OSR theory we can make several predictions: (i) Higher frequency of male-male competition is predicted for the balanced OSR treatment in comparison to the female-biased treatment, whereas the opposite is predicted for the frequency of female intrasexual competition; (ii) Similar to many other ungulate species, reindeer are polygynous and exhibit conventional sex roles; therefore, it is expected that males will engage in higher levels of intrasexual competition than females regardless of the OSR treatment, and (iii) The frequency of male courtship behaviour will either be lower in OSR = 1 because of higher male-male agonistic encounters or occur at higher frequencies due to the utilization of alternative mating tactics. Similar to various other taxa, male reindeer exhibit age-dependent differences in reproductive effort and mating tactic utilization, therefore the following predictions can be made on age specific responses: (i) Older males are expected to engage in higher intrasexual agonistic encounters compared to younger males in OSR = 1 and, (ii) Older males have the advantage of rutting experience, while 1.5-year-old males would be participating in their first breeding season; therefore, it is expected that courtship rate will be higher among the 2.5-year-old males.

METHODS

Study location and Research herd

Behavioural sampling occurred over the course of two field seasons, at the Kutuharju Experimental Reindeer Research Station maintained by the Reindeer Herder's Association, near Kaamanen in Northern Finland (69°N, 27°E). Sampling for the first field season utilized 2.5-year-old male reindeer and went from September 29th – October 15th, 2016. The second field season utilized 1.5-year-old male reindeer, and sampling went from October 1st, 2017 – October 17th, 2017. The station's total area is 45km^2, which is further subdivided into the following four areas: Lauluvaara, Sinioivi, Piskivaara and Maantielohko. Sinioivi (~15 km^2) and Lauluvaara (~13.8 km^2) are utilized during the rut. Two fenced enclosures were utilized for each field season, both with an area of 1km^2, and shared 0.4km of fencing. These areas are largely characterized by birch (*Betula spp.*) and Scots pine (*Pinus sylvestris*) forests, along with the presence of many bogs and lakes (L'Italien et al. 2012).

Experimental Design

The OSR was manipulated on two levels, where it was either a female biased OSR of 0.5 (3♂:6♀) or a balanced OSR of 1 (3♂:3♀), to investigate its impact on inter and intra-sexual competition. The OSR of reindeer under more natural conditions during the rut can range anywhere from 0.16 (highly female biased) to 0.995 (highly male biased; Weladji et al, 2017). Female ungulates typically exhibit a short and highly synchronous oestrus (de Vos, Brokx and Geist 1967); therefore, it is expected that the number of females in oestrus will follow an inverse U – shaped pattern. This results in many females being in oestrus during peak rut, and very few during early and late rut (Hirotani 1989). In a closed population, where the number of mature males remains constant, OSR is predicted to follow a U – shaped pattern, resulting in peak rut being female biased and both early and late rut being male biased. With this in consideration and due to the potential risk of injury to our males, we did not provide a male-biased OSR treatment.

For each field season, 6 male reindeer (either 1.5 or 2.5-years-old) and 27 female reindeer (mixed age) were utilized. To ensure that any effect of treatment on male behaviour was due to the OSR level, both male age and density were kept constant. Male reindeer utilized in each study year were fitted with very high frequency (VHF) collars to allow tracking of breeding groups in the enclosures with radio telemetry. Both field seasons consisted of three trials, each with a duration of 5 days, and were separated by an acclimation day. At the beginning of each trial, the same six males were haphazardly herded into either enclosure 1 or 2 by local reindeer herders, whereas 9 new females were haphazardly separated into either enclosure for each trial. Due to the relatively large-scale nature of this study, with many recording techniques and the use of two enclosures simultaneously, data was collected by two observers. Prior to the start of each field season, both observers agreed on descriptions of the behaviours to be examined and a shared ethogram was constructed (see Table 1.1). During this pre-field season time frame, data was collected simultaneously by both observers to calculate the index of concordance for behavioural sampling, ensuring both observers were recording the same behaviours (Martin and Bateson 2007). The index of concordance was 88% for behavioural sampling and 98.3% for focal sampling in the 2016 field season. For the 2017 field season, the index of concordance was 93% for behavioural sampling and 99.5% for focal sampling.

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 (Protocole number 30000303) and by the Animal Experiment Board in Finland (Protocole number ESAVI/7711/04.10.07/2016).

Oestrus synchronization

To ensure female receptivity, a two-injection protocol of estrumate® (cloprestenol sodium), a synthetic analogue of prostaglandin that promotes oestrus in cattle, was utilized (Johnson 1978; Hardin et al. 1980; Odde 1990). Females were injected intramuscularly with 1mL of estrumate (0.25mg cloprestenol) by a local veterinarian, which was followed by a 10-day lag period prior to receiving a second injection. After the second injection they were haphazardly herded into their experimental enclosures. In normal cycling cattle, oestrus is expected to occur 2-5 days following the second injection. It is also important to note that females were kept in a separate paddock away from males to ensure copulation did not occur before any trial commenced.

Mating tactics

Upon entry to the enclosure for either OSR treatment, the entry time and the time at which the first group is observed was recorded. This allowed us to have an average search time for the first group over the five days of each trial. A group was defined as a cluster of individuals within 100m of each other, comprised of two or more individuals that are highly synchronized in their activity, separated by 100m from another group (Body et al. 2014). Once a group was found, the sex ratio, which male was dominant, and the observed mating tactics were recorded. Mating tactics included the following strategies: 'Dominant', 'Wannabe', 'Satellite', and 'Sneaker' (Holand et al. 2012). Due to the fission-fusion dynamics of a group being plastic, if any individuals left or joined a group for longer than 10 minutes, a new group composition was recognized.

Behavioural sampling of Agonistic and Courtship behaviours

Throughout each day of a trial, behavioural sampling with continuous measuring for 15 minutes was carried out. For behavioural sampling to occur, half the group or more needed to be visible to the observer. The behaviours of interest for this sampling were: chase, spar, fight, displace, head threat, attempted copulation, copulation, mate guarding, bush thrashing, scent marking, sneaking, follow, court, herd, grunt and flehmen (Espmark 1964; Tennenhouse et al. 2012). For the purpose of statistical analysis, these behaviours were pooled by day and divided into the following two main categories: courtship (mate guarding, follow, court, herd, flehmen, attempted copulation, and copulation) and agonistic (chase, spar, fight, displace and head threat). Whether or not interactions between individuals were male-male (M:M), female-female (F:F), or male-female (M:F) was also recorded. The identity (IDs) of the reindeer involved for each interaction was also noted.

Focal Sampling

Throughout each day of a trial, focal sampling was conducted on randomly chosen, active males from a breeding group (Martin and Bateson 2007). An individual focal observation consisted of 15 minutes of observation. Behaviour was recorded every 15 seconds, which included walking, foraging, standing, resting or other (agonistic and courtship behaviour). If visual contact of the male was lost during the focal observation, the recording was stopped and the total time observed was noted. To estimate the amount of time spent engaging in a specific activity, the behavioural frequencies were divided by the total focal duration.

Statistical Analysis

Generalized linear mixed models (GLMMs) were used to investigate the intensity of intra- and inter-sexual interactions, and male focal behaviours by using the 'lme4' and 'glmmADMB' packages (Fournier et al. 2012; Skaug et al. 2013; Bates et al. 2015). Co-linearity between variables was assessed by calculating the variance inflation factor (VIF), where if VIF > 2.5, the predictors involved were removed from the model. Both OSR and male age were found to have VIF values of 1.0, therefore they were utilized as predictors. Applying a backwards step wise approach to model selection, we first assessed if any interaction terms were significant. If the interaction was non-significant, the term was dropped from the model. All models were fitted with a Poisson distribution and a log link function. If overdispersion was detected, the GLMMs were fitted with a negative binomial distribution.

Treatment group was defined as a group of reindeer from one OSR treatment in a specific trial. This will result in 12 treatment groups over 6 trials, allowing the ability to rule out any differences between treatment groups from non-independence of observations (Thiele and Markussen 2012). Defining the treatment group in the GLMMs is important since the same six males were used throughout each field season, where they are only shuffled between trials, not replaced. Regardless of the behaviour being analyzed, all of our GLMM models included treatment group as a random factor. Additionally, to control for differences in site conditions between field sampling periods, year was included as a random factor in all models. Specifically, with respect to the male focal behaviour models, Reindeer ID was included as a random factor to control for repeated measures of the same individuals.

In the agonistic encounter models (intrasexual & intersexual), the response variable was the daily pooled frequency occurrence of agonistic (counts), which included the following behaviours: displace, chase, spar, fight and head threat. These GLMMs assessed whether the response variable varied with OSR level (0.5 or 1), male age (1.5 or 2.5-years-old), sex (male or female), and the interaction terms. The courtship models included the pooled frequency of occurrence of courtship behaviours (attempted copulation, copulation, mate guarding, follow, court, herd, and flehmen) as the dependent variable. These GLMMs assessed whether male courtship varied between OSR treatments, male age, or if there was a significant interaction between the two.

Least squares mean pairwise comparison (Tukey family) was conducted to determine if the mean frequency of male mating tactics (Dominant, Wannabe, Satellite, and Sneaker; Holand et al. 2012) differed prior to investigating each tactic separately. After this step, individual models were made for each tactic, with their frequency of occurrence (counts) as the response variable. These models included some or all of the following explanatory variables: OSR (0.5 or 1), male age (1.5 or 2.5-years-old), and the interaction between the two.

The response variable for the focal behaviour models included the frequency of occurrence of either resting, walking, standing, foraging or other (agonistic and courtship) behaviours. These models investigated whether time allocation to maintenance (foraging and resting) or active (walking, standing, other) behaviour varied by either OSR treatment, male age or an interaction between the two. Prior to analysis of individual focal behaviours, a multivariate analysis of variance (MANOVA) was conducted as a precursor to see if differences existed between group means of all five focal behaviours.

All analyses were conducted using R version 3.3.3, with the significance level set as 0.05 (R Core Team 2017).

RESULTS

Agonistic Encounters

The frequency of male intrasexual agonistic encounters were not found to significantly vary with OSR treatment (estimate = 0.472, 95% CI = -0.24, 1.19; p = 0.20) or Male age (estimate = 0.19, 95% CI = -0.52, 0.91; p = 0.60; see Figure 1.1a); however, there was a non-significant trend for male-male agonistic encounters to be higher in OSR = 1 for the 2.5-year-old males (estimate = 0.87, 95% CI = -0.69, 4.1; p = 0.161). Female intrasexual agonistic encounters were found to occur at significantly lower frequencies in OSR = 1 (estimate = -0.94, 95% CI = -1.72, -0.182; p = 0.015; see Figure 1.1b). When comparing male and female intrasexual agonistic encounters, the interaction between OSR and Sex was found to be significant (estimate = 1.41, 95% CI = 0.75, 2.1; p < 0.001; see Figure 1.1c), suggesting that males and females engaged in differing frequencies of intrasexual agonistic encounters depending on the OSR level. Lastly, with respect to intersexual agonistic encounters, a significant main effect was found for OSR (estimate = -0.50, 95% CI = -0.85, -0.084; p = 0.017) and male age (estimate = 0.71, 95% CI = 0.32, 1.1; p<0.001; see Figure 1.1d).

Male Courtship

The frequency of occurrence of male courtship behaviours was not found to significantly vary with OSR treatment (estimate = - 0.014, 95% CI = -0.62, 0.59; p = 0.97). In contrast, a significant main effect was found for Male Age (estimate = 0.78, 95% CI = 0.07, 1.5; p = 0.031), with the 2.5-year-old males performing courting behaviours more than the 1.5-year-old males (see Figure 1.2).

Mating tactics

The least square means pairwise test revealed a significant difference for all pairwise comparisons of mating tactics, excluding the ‘Wannabe’ and ‘Sneaker’ tactic comparison (p=0.73; see Table 1.2). The ‘Dominant’ mating tactic was found to have the highest frequency of occurrence, followed by the ‘Satellite’ mating tactic (see Figure 1.3). The frequency of occurrence for the ‘Dominant’ mating tactic was not found to vary with OSR treatment (estimate = 0.0023, 95% CI = -0.67, 0.68; p = 0.99). The effect of male age on the ‘Dominant’ mating tactic had approached significance (estimate = 0.66, 95% CI = -0.034, 1.4; p = 0.062), suggesting a tendency for the 2.5-year-old males to engage in this tactic more than the 1.5-year-old males (see Figure 1.4). The 'Satellite' mating tactic was not found to vary with OSR treatment (estimate = -0.025, 95% CI = -0.73, 0.70; p = 0.94); however, male age had a significant effect (estimate = 0.89, 95% CI = 0.13, 1.6; p = 0.021), with 2.5-year-old males engaging in the tactic at higher frequencies than the 1.5-year-old males (see Figure 1.4). The frequency of occurrence for the wannabe tactic was not found to vary between OSR treatments (estimate = -0.011, 95% CI = -1.6, 1.6; p = 0.99) or male age (estimate = 1.57, 95% CI = -0.57, 3.7; p = 0.15; see Figure 1.3). Finally, the sneaking tactic was not found to vary between OSR treatments (estimate = 0.67, 95% CI = -1.7, 3.1; p = 0.58) or male age (estimate = 0.67, 95% CI = -1.7, 3.1; p = 0.58; see Figure 1.3).

Average Activity Budget Frequencies

In total, 138 and 139 focal samples were completed for the 1.5-year-old and 2.5-year-old male reindeer, respectively. On average, across all trials and independent of OSR treatments, both 1.5 and 2.5-year-old males were found allocate most of their time towards foraging, making up 54.7% and 48.5% of their activity budget's respectively. Both 1.5 and 2.5-year-old males allocated the least amount of time towards engaging in the other behavioural category, making up 4.9% and 2.3% of their activity budget, respectively. Both walking and standing behaviour received higher time allocation by the 2.5-year-old males, making up 24.7% and 15.1% of their activity budget. In comparison, 1.5-year-old males allocated 17.0% and 14.2% of their time towards walking and standing behaviour. Resting behaviour occurred at comparable frequencies for both 1.5 and 2.5-year-old males, making up 9.2% and 9.6% of their overall activity budget, respectively (see Figure 1.5). The MANOVA analysis yielded a significant interaction between OSR and male age, suggesting that the mean frequency of each focal behaviour varies depending on the level of OSR and male age ($F_{(269)} = 2.99$, $p = 0.012$).

Resting Behaviour

The average frequency of occurrence (counts) for resting behaviour in the female biased OSR treatment for the 1.5-year-old males was found to be 6.4 ± 1.76 (SE) and 7.42 ± 1.85 (SE) for the 2.5-year-old males. Resting behaviour was lower in the balanced OSR treatment, with the average count for the 1.5-year-old males being 4.74 ± 1.53 and 3.92 ± 1.40 for the 2.5-year-old males. There was no significant effect of OSR treatment (estimate = -0.10, 95% CI = -0.47, 0.26; p = 0.59) or male age (estimate = 0.003, 95% CI = -0.36, 0.36; p = 0.99) on the frequency of occurrence of resting behaviour in male reindeer (see Figure 1.6).

Walking Behaviour

The average count for walking behaviour in the female biased OSR treatment for the 1.5-year-old males was found to be 10.20 ± 0.91 (SE) and 7.60 ± 0.75 (SE) for the 2.5-year-old males, whereas in the balanced OSR treatment the average count for the 1.5-year-old males was 10.30 ± 1.06 (SE) and 10.70 ± 1.01 (SE) for the 2.5-year-old males. The frequency of occurrence of walking behaviour did not differ between OSR treatments (estimate = 0.16, 95% CI = -0.093, 0.42; p = 0.21) or with male age (estimate = -0.14, 95% CI = -0.40, 0.11; p = 0.28; see Figure 1.6).

Standing Behaviour

In the female biased OSR, the average count for standing behaviour for the 1.5-year-old males was found to be 8.45 ± 1.12 (SE) and 10.10 ± 0.96 (SE) for the 2.5-year-old males. In the balanced OSR, the average count for 1.5-year-old males was 8.62 ± 0.99 and 19.76 ± 1.93 for the 2.5-year-old males. The interaction between OSR treatment and male age approached significance (estimate = 0.72, 95% CI = -0.047, 1.5; p = 0.066), with a non-significant main effect of OSR treatment (estimate = -0.053, 95% CI = -0.60, 0.50; p = 0.85) and male age (estimate = 0.184, 95% CI = -0.05, 1.5; p = 0.51; see Figure 1.6). Upon investigation of each age class separately, standing behaviour was found to not significantly differ between OSR treatments for 1.5-year-old males (estimate = -0.063, 95% CI = -0.80, 0.70; p = 0.86). In contrast, the frequency of occurrence for standing behaviour was found to occur at significantly higher frequencies in OSR = 1 for the 2.5-year-old males (estimate = 0.71, 95% CI = 0.40, 1.0; $p<0.001$).

Foraging Behaviour

In the female biased OSR, the average count for foraging behaviour for the 1.5-year-old males was found to be 31.5 ± 1.87 (SE) and 33.4 ± 1.79 (SE) for the 2.5-year-old males. In the balanced OSR, the average count for 1.5-year-old males was 33.9 ± 1.96 and 24.4 ± 2.13 for the

2.5-year-old males. The interaction between OSR and male age was found to be significant (estimate = - 0.39, 95% CI = -0.71, -0.070; p = 0.018; see Figure 1.6). When examining each age class separately, there was no significant relationship between OSR treatment and the frequency of occurrence of foraging behaviour in the 1.5-year-old males (estimate = 0.075, 95% CI = -0.20, 0.35; p = 0.60), however, the 2.5-year-old males were found to forage at significantly lower frequencies in the OSR = 1 treatment (estimate = -0.31, 95% CI = -0.55, -0.073; p = 0.011).

Other Behaviour

In the female biased OSR, the average count for other behaviour for the 1.5-year-old males was found to be 3.53 ± 0.90 (SE) and 1.53 ± 0.38 (SE) for the 2.5-year-old males. In the balanced OSR, the average count for 1.5-year-old males was 2.40 ± 0.66 and 1.26 ± 0.72 for the 2.5-year-old males. OSR treatment was not found to have a significant main effect on the frequency of other behaviour (estimate = -0.27, 95% CI = -0.80, 0.25; p = 0.30), however, a significant relationship between male age and the frequency of occurrence of other behaviour was found (estimate = - 0.91, 95% CI = -1.4, -0.40; p<0.001), suggesting that the 1.5-year-old males engaged in higher frequencies of other behaviour than the 2.5-year-old males (see Figure 1.6).

DISCUSSION

We predicted that in the balanced OSR treatment, the frequency of female-female agonistic encounters would be lower, in comparison to the female-biased OSR treatment. Conversely, we predicted that the frequency of male-male agonistic encounters would be higher in the balanced treatment, in comparison to the female-biased OSR treatment. We found significant support for there to be a higher frequency of female-female agonistic encounters in the female biased OSR vs the balanced OSR. It is important to acknowledge, that while we did observe this significant effect, we did not control for female density or absolute density, therefore it is difficult to conclude that this effect was entirely due to OSR and not a density related effect or an interaction between the two.

Classical OSR theory predicts that as the OSR becomes increasingly more biased towards one sex, there will be increased intrasexual competition for mates by the more abundant sex (Emlen and Oring 1977; Kvarnemo and Ahnesjo 1996). To date, there have been very few studies that investigate both male and female competitive behaviour simultaneously; however, our results along with the available evidence in the literature provides support for the prediction that female-female agonistic encounters will increase as the OSR becomes more female biased. In fact, this trend has been seen across a variety of species, such as sand gobies *Pomatoschistus minutus* (Kvarnemo et al. 1995), the European lobster *Homarus gammarus* (Debuse et al. 1999), Japanese medaka *Oryzias latipes* (Grant and Foam 2002), two-spotted goby, and guppies *Poecilia reticulata* (Chuard et al. 2016).

Traditionally, sexual selection studies in the past have mainly focused on mating competition among males, ignoring the female aspect. This is largely due to the conventional assumption that female reproductive success is mainly constrained by resources other than mates, whereas due to the higher potential reproductive rate among males, OSR is typically biased towards males, resulting in mates being the limiting factor to them (Clutton-Brock and Vincent 1991). Indeed, among female mammals, there are high energetic costs associated with maternal investment, such as with gestation and lactation, resulting in direct resource competition among females (Rosvall 2011). However, it has been shown that females, like males, do compete for access to mates, through activities such as threat displays (ex: Vervet monkeys, *Chlorocebus pygerythrus*; Horrocks & Hunte 1983), punishment (ex: Cleaner wrasse, *Labroides dimidiatus* ; Raihani, Grutter and Bshary 2010), harassment (ex: Gelada baboons, *Theropithecus gelada*; Dunbar and Dunbar 1977), reproductive suppression (ex: Damaraland mole rat, *Fukomys damarensis*; Young et al. 2010), and less commonly, fights (ex: Meerkats, *Suricata suricatta*; Sharp & Clutton-Brock 2011; Clutton-Brock and Huchard 2013). In some ungulates that exhibit harem defense during a well-defined mating season, it is common for there to be synchrony of receptivity among females, resulting in competition among females for the attention of males (Bro-Jorgensen 2002, 2011). A strong case for evidence that mate limitation could drive female competition, as predicted by OSR theory, was observed in the saiga antelope (*Saiga tatarica*), after poaching created a heavily biased sex ratio towards females, resulting in dominant females excluding subdominant females from mating (Milner-Gulland et al. 2003).

It has been suggested that one of the main causes for female-female mate competition among ungulate species arises from sperm limitation, occurring from males engaging in high rates of mating during peaks of rutting activity. Sperm limitation is promoted by factors such as female promiscuity, synchronized breeding and also strong female mate preferences, resulting in fewer males being considered as eligible mates (Ahnesjo et al. 2001; Bro-Jorgensen 2011). Female reindeer/caribou, exhibit a short and highly synchronous oestrus, with most females entering oestrous during peak rut. Approximately 90% of females are successfully copulated in a 10-21-day period, with calving occurring in a highly synchronized manner the following spring (Dauphiné and McClure 1974; Bergerud 1975; Ropstad et al. 1996; Rowell and Shipka 2009).

Males in this study's herd typically copulate with females during peak rut (Weladji et al. 2017). We found that 2.5-year-old males engaged on average in more courting behaviours on day 2 of each trial, coinciding with when oestrus was expected to be induced for most of our females. It is plausible that the higher female-female agonistic encounters we observed during the female biased OSR supports the idea of females competing for the (best) mate. Thus, such agonistic encounters between females could be functioning as a way to gain the attention of desired mates. A similar proposal has been made with the topi antelope (*Damaliscus lunatus jimela*), where oestrous females engaged in higher frequencies of aggressive acts, increasing their chance of mating (Bro-Jorgensen 2007).

Contrary to OSR theory, we did not find support for the prediction that agonistic encounters between males would occur at higher frequencies in OSR = 1 or that age was an important factor. However, with the 2.5-year-old males we did note a non-significant trend for male-male agonistic encounters to occur at higher frequencies in the OSR = 1 treatment. An important limitation to note here is that our confidence intervals for our male intrasexual results were quite large, suggesting we may have lacked sufficient power to accurately detect variation in male-male agonistic encounters between treatments due to our study having few replicates. Lastly, we also recognize that due to our sampling occurring over the course of two field seasons, differing environmental variables could have a confounding effect with male age. Outside of these limitations, it is also plausible that our lack of support for OSR influencing intrasexual competition among male reindeer could be adding to evidence that suggests the predictive effects of OSR on mate competition varies between species and may not be as generalizable as previously thought (ex: Balshine-Earn 1996; Wacker et al. 2013; de Jong et al. 2009).

When comparing between the sexes for the frequency of occurrence for intrasexual agonistic encounters, a significant interaction between OSR and sex was present. The importance of this interaction term is two-fold with respect to supporting conventional sex roles: (1) Regardless of the OSR level, males engaged in more intrasexual agonistic encounters than females, and (2) Males and females were responding to changes in OSR differently, such that in the OSR = 1 treatment, male intrasexual agonistic encounters occurred at higher frequencies, while female intrasexual agonistic encounters occurred at lower frequencies. Conventional sex roles dictate that males are more competitive and mate randomly, whereas females are more passive and choosy (Houde 2001). These roles are thought to evolve due to sex-specific differences in reproductive physiology, where the low cost of sperm production and a lack of paternal care, allows for a greater number of ready to mate males than available females in a population's mating pool (Emlen and Oring 1977; Clutton-Brock and Vincent 1991). Consequently, the energetic costs of reproduction impose a selection pressure for females to be choosy when selecting a mate to improve the chance of getting a high-quality male. In contrast, the lack of reproductive physiological constraints in males, imposes a selection pressure for them to increase their potential reproductive success by maximizing the number of mates they obtain. Previous literature has also shown that most female reindeer mate with the highest ranking and largest males (Røed et al. 2002), further supporting the presence of conventional sex roles in this species.

Furthermore, within the literature there is a discrepancy in courtship results when comparing laboratory and field studies (see De Jong et al., 2009). Typically, field studies support the idea that OSR regulates mating competition, whereas laboratory studies commonly report results that appear contradictory to traditional OSR theory. A meta-analysis by Weir et al. (2011) revealed that competitive behaviours do not always linearly increase with an increasing OSR bias towards the competitor's own sex. This result highlights that the nature of the relationship is context dependent on the form of mating behaviour being investigated. Denoël et al. (2005) did not report significant differences in courting behaviour and agonistic encounters of alpine newt (*Triturus alpestris*) males between male-biased OSRs or balanced OSRs. Similarly, we did not find OSR to significantly influence male courtship or mating tactics. However, we did find that male age was significantly influencing the frequency of courting behaviour, with 2.5-year-old males engaging in higher frequencies of courting behaviour regardless of the OSR treatment. Additionally, male age was also found to be an important consideration regarding the frequency of the 'Satellite' mating tactic and to a lesser extent, the 'Dominant' mating tactic. The 'Dominant' mating tactic was found to occur more frequently than any other tactic, followed by the 'Satellite' mating tactic; both of which occurred at higher rates in the 2.5-year-old males.

Under more natural settings with animal societies containing mixed age groups, age-dependent mating tactics have been observed across a wide variety of taxa (Gross 1996; Taborsky 2008), including various ungulate species (Hogg and Forbes 1997; Saunders et al. 2005; Mainguy et al. 2008; Willisch and Neuhaus 2009). Typically, in these mixed age societies, older males utilize the more dominant strategy and subordinate males (usually younger in age) utilize alternative tactics. Similar to many other ungulate species: e.g., red deer, *Cervus elaphus* (Clutton-Brock and Albon 1979), Burchell's zebra, *Equus burchellii* (Schilder 1992), Elk, *Cervus canadensis* (Struhsaker 1967), reindeer exhibit harem defense polygyny, where the gregariousness of females allows males to directly monopolize them through coercion and deception (Emlen and Oring 1977; Bro-Jorgensen 2011). Commonly, the 'Dominant' mating tactic is utilized by higher ranking older males, while lower ranked prime age males utilize the 'Wannabe' and 'Satellite' mating tactics, leaving the younger males to utilize the 'Sneaking' mating tactic (Holand et al. 2012). It is likely that higher male courtship and use of the 'Dominant' mating strategies by our 2.5-year-old males reflects the advantage of their previous rutting experience. Furthermore, with the absence of a mixed age structure, it is reasonable that our males recognized that there was a lower risk of being outcompeted by older males. By taking advantage of this situation, they could attempt to acquire females utilizing the 'Dominant' mating tactic instead of relying on less risky tactics like sneaking (Mysterud et al. 2003). Thus explaining why the Dominant mating tactic was the most frequently occurring mating tactic.

Moreover, it was recently suggested that due to the dynamic nature of OSR during the reindeer rutting season, the intensity of mating competition may not be a main driver for male mating behaviour. This was supported by the observation that male mating behaviour followed a pattern of adjustment in accordance with the time of the rut and social environment (Weladji et al, 2017). Our results along with a growing body of evidence could be highlighting that the importance of OSR as a predictor for mating competition and mating system structure may vary between species. Further suggesting that other factors should be considered along with OSR as researchers attempt to expand classic predictions across various taxa. In fact, a myriad of other factors impact competition for mates, such as mortality (Okuda 1999), the cost of reproduction (Kokko and Monaghan 2001), mate quality (Johnstone et al. 1996) and density (Kokko and Rankin 2006). Specifically, with respect to males of polygynous mammalian species, two of the main determinants of mating success are social rank and male age (McElligott et al. 1998; Pelletier and Festa-Bianchet 2006).

In polygynous mammals, it is typical for males to begin their reproductive life later than females, which is considered a by-product of male intrasexual competition for mates (Bergerud 1974; Clutton-Brock et al. 1982). Reproductive success varies greatly among polygynous males, with social rank being a key determining factor in the number of mates they can acquire, which varies with body weight, age, and weapon size (Barrette and Vandal 1986; Melnycky et al. 2013). Among male reindeer it has been shown that their reproductive success is highly skewed, with the older more dominant individuals siring the most calves (Røed et al. 2002). Sex ratio has also been found to be an important factor for influencing variance in male reindeer reproductive success. As the ratio becomes more balanced, older dominant males switch from guarding large groups of females to restricting access to individual females that are in oestrus (Røed et al. 2002). Commonly, yearling male reindeer begin to develop secondary sexual characteristics within the first 4-8 months (Leader-Williams 1980). However, histological investigations of reindeer testes and epididymes found that sexual maturity is not reached until 17-18 months, suggesting that during their first rut they would not be considered sexually mature (McEwan 1963).

Independent of OSR treatment, our males spent the majority of their time engaging in foraging behaviour, with 1.5 and 2.5-year-old males allocating ~ 55% and 48% of their time towards foraging, respectively. Comparatively, previous literature has found that during the rut, female reindeer allocate ~75% of their time towards engaging in foraging behaviour (Djakovic et al. 2015), highlighting differing life history strategies for both sexes. Similar to reindeer, it has been shown in other ungulate species, such as feral goat (*Capra hircus*) and fallow deer, that females do not change their foraging behaviour during the rut, likely reflecting the mixture of capital and income breeding strategy they impose to offset the costs of reproduction (Pelabon and Komers 1997; Shi et al. 2003). In contrast, male reindeer impose a capital breeding strategy, where they dramatically reduce their foraging during the rut period, prioritizing time allocation towards behaviours that will increase their potential reproductive success (Espmark 1964).

In northern ungulate species, the rutting period is usually short; therefore, males favour time allocation towards mating activities over maintenance activities. This brief period of high energy expenditure occurs prior to a harsh winter, characterized by lower forage quality and availability (Coulson et al. 2001). Winter mortality among ungulate species has been observed to be higher for prime-aged males than younger individuals, where this difference in mortality has been associated with the energetic costs of engaging in intense mating behaviour during the brief rutting season (Festa-Bianchet 1989; Ditchkoff et al. 2001).

A key determining factor in both competitive ability and lifetime reproductive success of male ungulates is their social rank, which varies with body weight and condition, age, and weapon size (Barrette and Vandal 1986; Melnycky et al. 2013). Thus, heavier prime-aged males commonly have higher reproductive success and are the harem holders (Mysterud et al. 2001), experiencing greater somatic costs (Skogland 1989; Mysterud et al. 2005). Given that harsh winter conditions follow the rutting season, it may still be more beneficial for non-peak aged males to invest towards maximizing their body size to facilitate growth and minimize susceptibility towards mortality during the winter, even when presented mating opportunities in the absence of older males, like we provided in this study, explaining the lack of difference in foraging behaviour between OSR treatments for the 1.5-year-old males.

Standing behaviour was also found to significantly differ between OSR treatments for the 2.5-year-old males, where standing occurred at higher frequencies in OSR = 1; however, no change was noted for the 1.5-year-old males. Vigilance behaviour in mammals has been associated with various functions, such as predator detection (Hunter and Skinner 1998; Creel et al. 2014), search of forage (Caro 1987; Coolen et al. 2001), or to monitor competitors during the breeding season (Alados 1985). Among ungulate species, vigilance has been mainly attributed to anti-predator avoidance (Hunter and Skinner 1998); however, it has been suggested that vigilance during the breeding season can function as a way for males to monitor potential competitors and mates (Underwood 1982; Reboreda and Fernandez 1997; Cameron and Du Toit 2005). The observed higher frequency of standing behaviour in OSR =1 for our 2.5-year-old males could be indicative of male reindeer paying more attention to other subordinate males to ensure they do not gain access to the few females available.

In summary, we found support for predictions based on OSR theory with respect to female-female agonistic encounters occurring at lower frequencies in OSR = 1; however, we found no support for the prediction that male-male agonistic encounters would occur at greater frequencies of occurrence in OSR = 1. We did find support for our prediction of conventional sex roles based on OSR theory, where the frequency of occurrence of intrasexual agonistic encounters varied based on the reindeer being male or female and the OSR treatment involved, with males engaging in higher frequencies overall. While we did not find support for our prediction that male courtship would either have lower frequencies of occurrence in OSR = 1 due to a rise in male-male agonistic encounters or have higher frequencies of occurrence due to the adoption of alternative mating tactics, we did find support for our prediction that older males would engage in higher frequencies of courting behaviour. Independent of OSR and male age, the most common male mating tactic was the ‘Dominant’ mating tactic, which is expected in a strongly polygynous species such as reindeer, with harem formation during the rut.

Although we did observe some support of prevailing OSR theory, our results on male-male agonistic and male courtship add to a growing body of evidence in the literature showcasing that the predicted positive relationship between mating competition and OSR may be an oversimplification (Klug et al., 2010), such that the value of OSR as a predictor of mating competition likely varies between species and ecological conditions. Our emerging trends based on male age cohort comparison, further highlight the importance of considering other factors that impact competition for mates, such as prime reproductive age. This is especially true for future research aiming to expand the generalizability of OSR theory to a wider range of taxa and ecological conditions.

TABLES AND FIGURES

Table 1.1: An ethogram of agonistic and courtship behaviours exhibited by reindeer (*Rangifer tarandus*) of a semi-domesticated population in Kaamanen, northern Finland, inspired by Espmark (1964) and Tennenhouse et al. (2012). Reproductive behaviour data based on this ethogram was collected using scan sampling, over the course of two rutting seasons, from September 29th – October 15th, 2016, and October 1st – October 17th, 2017.

Behaviour	Description	Codes
Rest	Lying down, sleeping or ruminating	**R**
Stand	Standing and not showing any movement behaviour or foraging behaviour	**S**
Walk	Slow movement	**W**
Foraging	Eating behaviour	**E**
Chase	Perusing another individual, with either one or both exhibiting aggression and or/ submission	**C**
Herding	Perusing a female until she returns to the mating group	**H**
Spar	Short bouts of fighting behaviour	**SP**
Displace	One individual approaches another, and that individual retreats	**D**
Court	Following a female or walking beside her while performing mating behaviours	**CO**
Copulation attempt	Mounting without copulation	**AC**
Copulation	Mounting with pelvic thrusting	**COP**
Bush thrashing	The rubbing of antlers against shrubs or small flexible trees	**BT**
Sneaking	Staying in the outskirts of a group and gaining access to females while the dominant male is engaged in another mating tactic or agonistic.	**SK**
Scent marking	Urination on hind legs	**SM**
Head threat	Shaking of head to show off antlers (can lead to	**HT**

	displacement)	
Grunting	A series of low sounding, husky, rapid rattles, which are brought about by frequent expirations of air.	**G**
Follow	Following an individual (behind them)	**FO**
Flehmen	The upper lip is curled, nose is wrinkled and the head is raised and stretched forward. Tongue undulations are made directed towards a female.	**FL**
Mate Guarding	Keeping other males away from a female. Following her, side by side.	**MG**

Table 1.2: The least squares mean pairwise comparisons (Tukey family) of male reindeer (*Rangifer tarandus*) mating tactics (Dominance, Satellite, Wannabe, Sneaker), independent of OSR or male age. The mating tactic data was collected over the course of two rutting seasons, September 29th – October 15th, 2016, & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

Pairwise Comparison	Estimate	± Standard Error	p-value
Satellite – Dominance	0.80	0.16	< 0.001
Sneaker – Dominance	3.73	0.58	< 0.001
Wannabe – Dominance	3.04	0.41	< 0.001
Sneaker – Satellite	2.93	0.58	< 0.001
Wannabe – Satellite	2.23	0.42	< 0.001
Wannabe – Sneaker	- 0.69	0.82	0.83

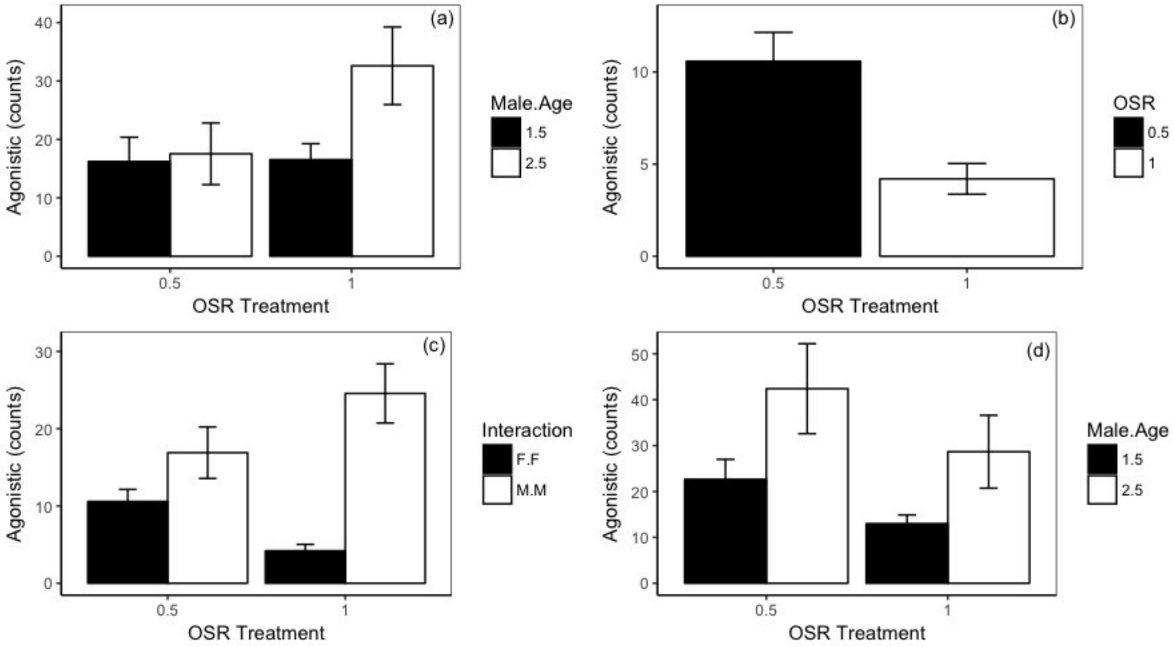

Figure 1.1: The average frequency of occurrence (counts) of pooled agonistic behaviours (displacement, chase, spar, fight and head threat) ± 1 standard error (SE) of male (1.5 or 2.5 years old) or female (mixed age) reindeer (*Rangifer tarandus*) between OSR treatments: (a) The relationship between male-male agonistic encounters, OSR and male age, (b) The relationship between female-female agonistic encounters and OSR, (c) A comparison of male and female intrasexual agonistic encounters in relation to OSR, and (d) The relationship between intersexual agonistic encounters, OSR and male age. The agonistic data was collected over the course of two rutting seasons, September 29th – October 15th, 2016, and October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

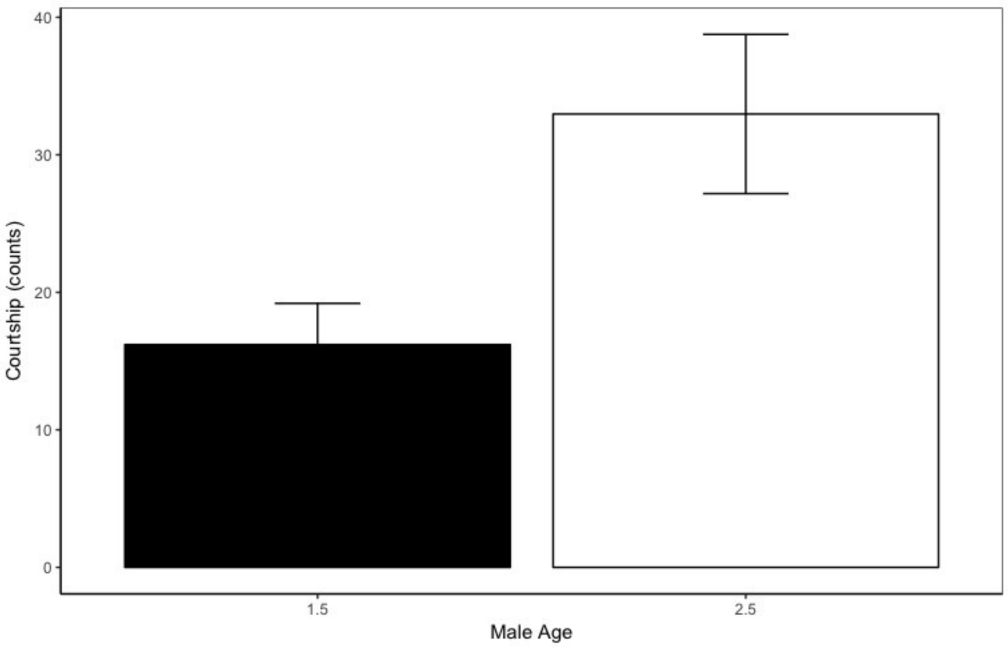

Figure 1.2: The average frequency of occurrence (counts) of pooled courtship behaviours (attempted copulation, copulation, mate guarding, follow, court, herd and flehmen) ± 1 standard error (SE) of mixed age female and either 1.5 or 2.5-year-old male reindeer (*Rangifer tarandus*), independent of OSR. The male courtship data was collected over the course of two rutting seasons, September 29th – October 15th, 2016 & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

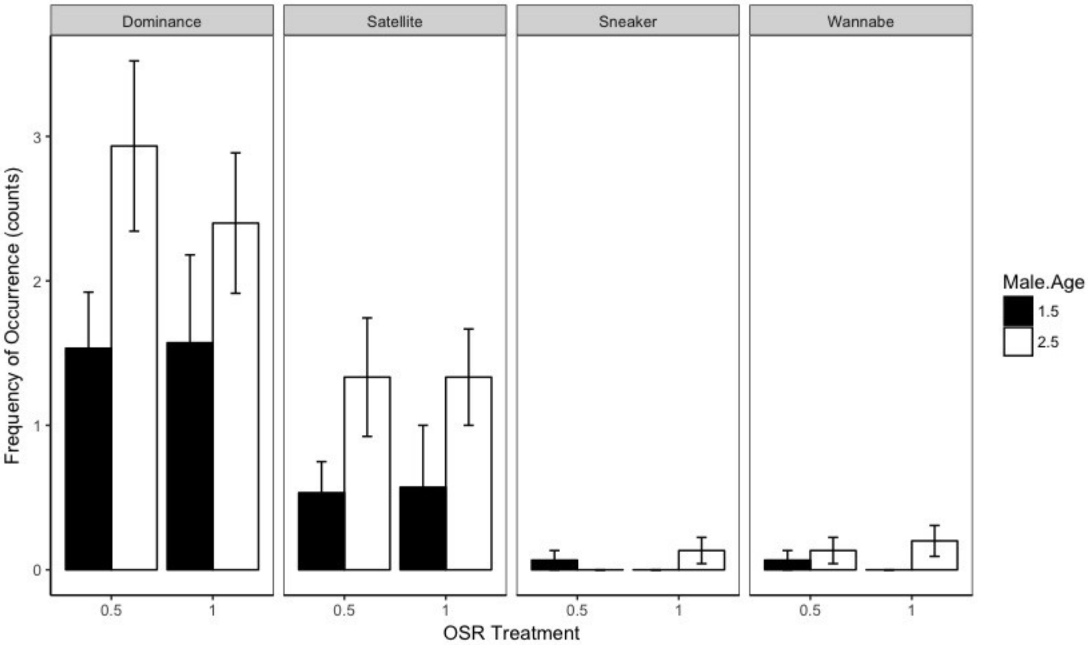

Figure 1.3: The average frequency of occurrence (count) of mating tactics (Dominance, Satellite, Sneaker, Wannabe) ± 1 standard error (SE) per OSR treatment (0.5 or 1) for both 1.5 and 2.5-year-old male reindeer (*Rangifer tarandus*) over the course of three trials (N=3), each lasting 5 days. The male mating tactic data was collected over the course of two rutting seasons, September 29th – October 15th, 2016 & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

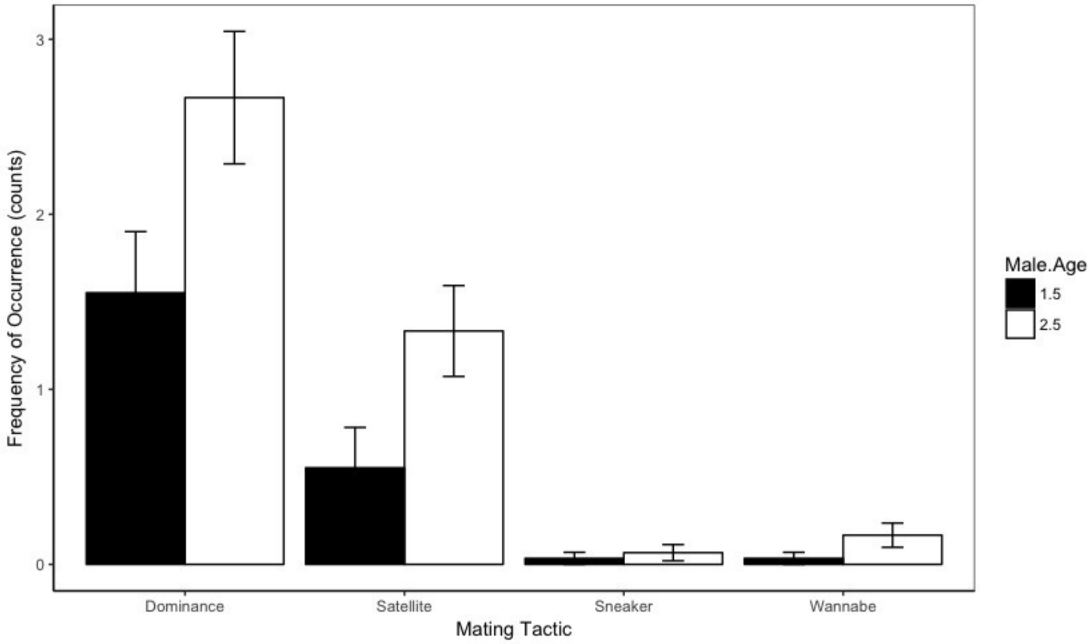

Figure 1.4: The average frequency of occurrence (count) of mating tactics (Dominance, Satellite, Sneaker, Wannabe) ± 1 standard error (SE), independent of OSR treatment, for both 1.5 and 2.5-year-old male reindeer (*Rangifer tarandus*) over the course of three trials (N=3), each lasting 5 days. The behavioural data was collected over the course of two rutting seasons, September 29th – October 15th, 2016 & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

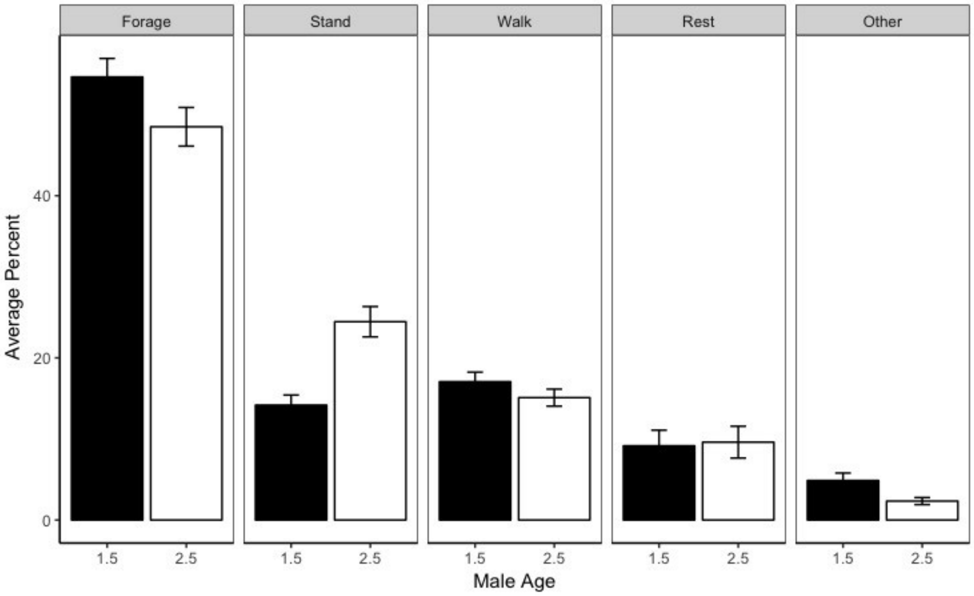

Figure 1.5: The average time allocated to the following focal behaviours: Forage, Stand, Walk, Rest or Other (includes agonistic and courtship behaviours) ± 1 standard error (SE), for 1.5-year-old and 2.5-year-old male reindeer (*Rangifer tarandus*) independent of OSR level. The activity budget data was collected using the focal sampling technique (15 min = 60 sampling events per every 15s), over the course of two rutting seasons, September 29th – October 15th, 2016, & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

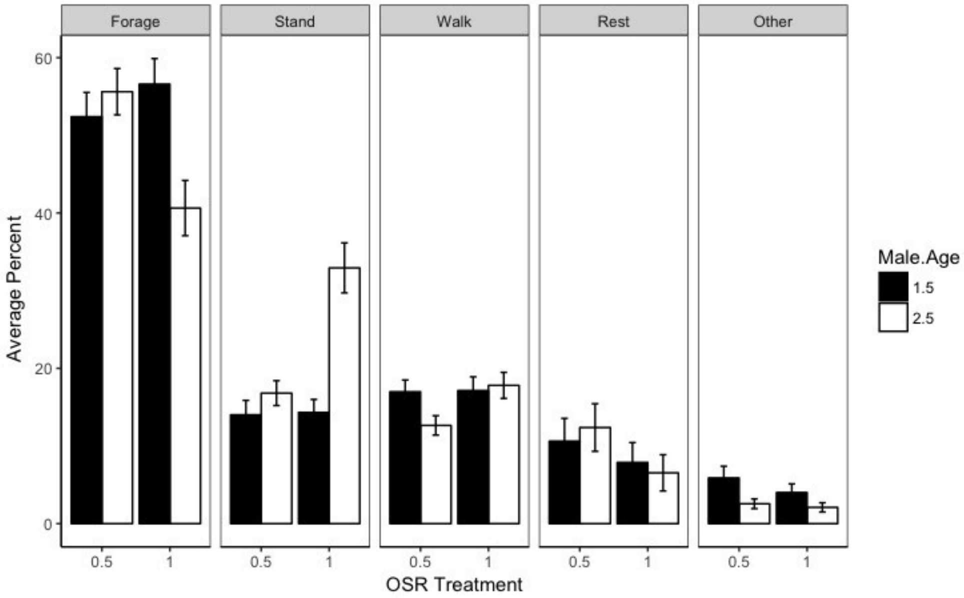

Figure 1.6: The average time allocated to the following focal behaviours: Forage, Stand, Walk, Rest or Other (includes agonistic and courtship behaviours) ± 1 standard error (SE), for 1.5-year-old and 2.5-year-old male reindeer (*Rangifer tarandus*) in either a female biased OSR (3♂:6♀ = OSR 0.5) or a balanced OSR (3♂:3♀ = OSR 1). The activity budget data was collected using the focal sampling technique (15 min = 60 sampling events per every 15s), over the course of two rutting seasons, September 29th – October 15th, 2016, & October 1st – October 17th, 2017, at the Kutuharju Experimental Reindeer Research Station in Kaamanen, Finland.

GENERAL CONCLUSIONS

Overall, OSR predictions regarding mating competition have been supported in the literature, with much of the experimental work mainly dealing with males of small bodied taxa in laboratory settings (Weir et al. 2011). To the best of our knowledge, the studies contained in this thesis, are one of the first to have explored how an experimentally manipulated OSR influences mating behaviour in a large mammalian species, under semi natural conditions.

We did find some support for prevailing OSR theory, notably regarding our female intrasexual agonistic encounter and our comparison of how male and female reindeer respond to shifts in OSR, however, our lack of support for our predictions on male mating competition results raises some caution for studies only using OSR as a metric for the strength of sexual selection. In both of our age groups, there was no significant difference in the level of male-male competition as OSR increased; however, there was an observed non-significant trend for competition to increase with OSR in the older age group. This result coupled with the lack of any emerging trend in how 1.5-year-old males respond to changes in OSR, the increase in courtship behaviour with age, and the observed significant increase in vigilance behaviour and decrease in foraging behaviour as OSR increases for the 2.5-year-old males, further highlights the importance of considering male age in this species. These results also further support the suggestion that OSR may potentially not be a highly important factor influencing mating competition in this particular species (Weladji et al. 2017).

Furthermore, the evidence we presented here, highlighting age contrasts in behavioural maturity of our males, may serve as a cautionary piece of information for herd management. While, male reindeer are technically sexually mature by 17-18 months old, their lack of previous rutting experience typically leaves them at a disadvantage with respect to acquiring mates. Maintaining young male age class structure and female biased sex ratios, may potentially result in younger males not properly developing strong rutting strategies due to the lack of older and experienced individuals to learn from, which can lead to delays in calving, lower birth synchrony, delay the development of body mass, and shifts in offspring sex ratio (Milner et al. 2007).

In conclusion, we did find some promising trends in support of OSR theory, however, our results suggest that future studies aiming to expand the generalizability of experimental OSR literature to underrepresented taxa, like mammals, need to consider other factors that influence the ability of individuals to respond to different levels of OSR, like prime age of the species.

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APPENDIX

Appendix A: These matrices contain the male-male agonistic encounters between the three 1.5-year-old males present in either a balanced (1) or female-biased (0.5) OSR, for every trial (N=3). If read from left to right, the values for each reindeer ID represent the number of agonistic encounters that individual won against the male in the same column as the value. If read from top to bottom, the values for each reindeer ID represent the number of agonistic encounters that individual lost to the male in the same row as the value.

Trial 1 OSR 0.5	Va K233	Va K207	Va K230
Va K233	*	0	8
Va K207	7	*	7
Va K230	1	0	*

Trial 1 OSR 1	7794	Va K217	Va K261
7794	*	6	0
Va K217	4	*	0
Va K261	14	20	*

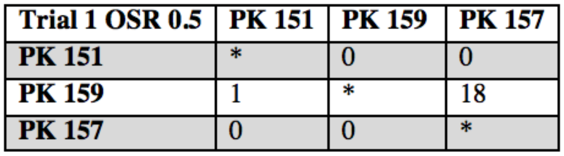
Trial 2 OSR 0.5	Va K261	Va K207	Va K233
Va K261	*	24	9
Va K207	5	*	5
Va K233	0	0	*

Trial 2 OSR 1	7794	Va K230	Va K217
7794	*	6	22
Va K230	1	*	4
Va K217	1	1	*

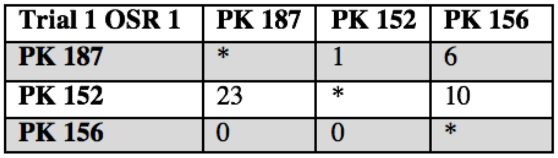
Trial 3 OSR 0.5	7794	Va K233	Va K217
7794	*	23	8
Va K233	0	*	8
Va K217	0	1	*

Trial 3 OSR 1	Va K230	Va K207	Va K261
Va K230	*	1	0
Va K207	5	*	1
Va K261	13	14	*

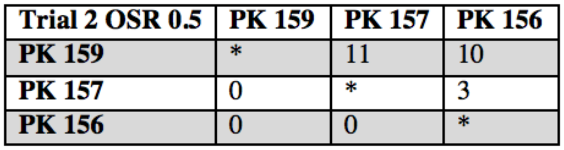
Appendix B: These matrices contain the male-male agonistic encounters between the three 2.5-year-old males present in either a balanced (1) or female-biased (0.5) OSR, for every trial (N=3). If read from left to right, the values for each reindeer ID represent the number of agonistic encounters that individual won against the male in the same column as the value. If read from top to bottom, the values for each reindeer ID represent the number of agonistic encounters that individual lost to the male in the same row as the value.



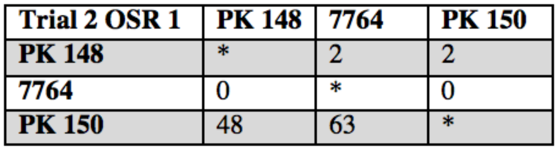
Trial 1 OSR 0.5	**PK 151**	**PK 159**	**PK 157**
PK 151	*	0	0
PK 159	1	*	18
PK 157	0	0	*



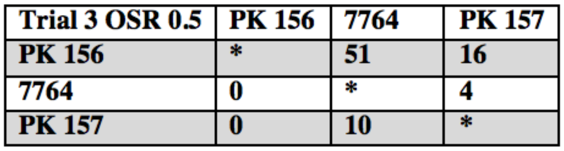
Trial 1 OSR 1	**PK 187**	**PK 152**	**PK 156**
PK 187	*	1	6
PK 152	23	*	10
PK 156	0	0	*



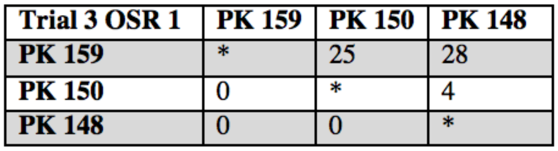
Trial 2 OSR 0.5	**PK 159**	**PK 157**	**PK 156**
PK 159	*	11	10
PK 157	0	*	3
PK 156	0	0	*



Trial 2 OSR 1	**PK 148**	**7764**	**PK 150**
PK 148	*	2	2
7764	0	*	0
PK 150	48	63	*

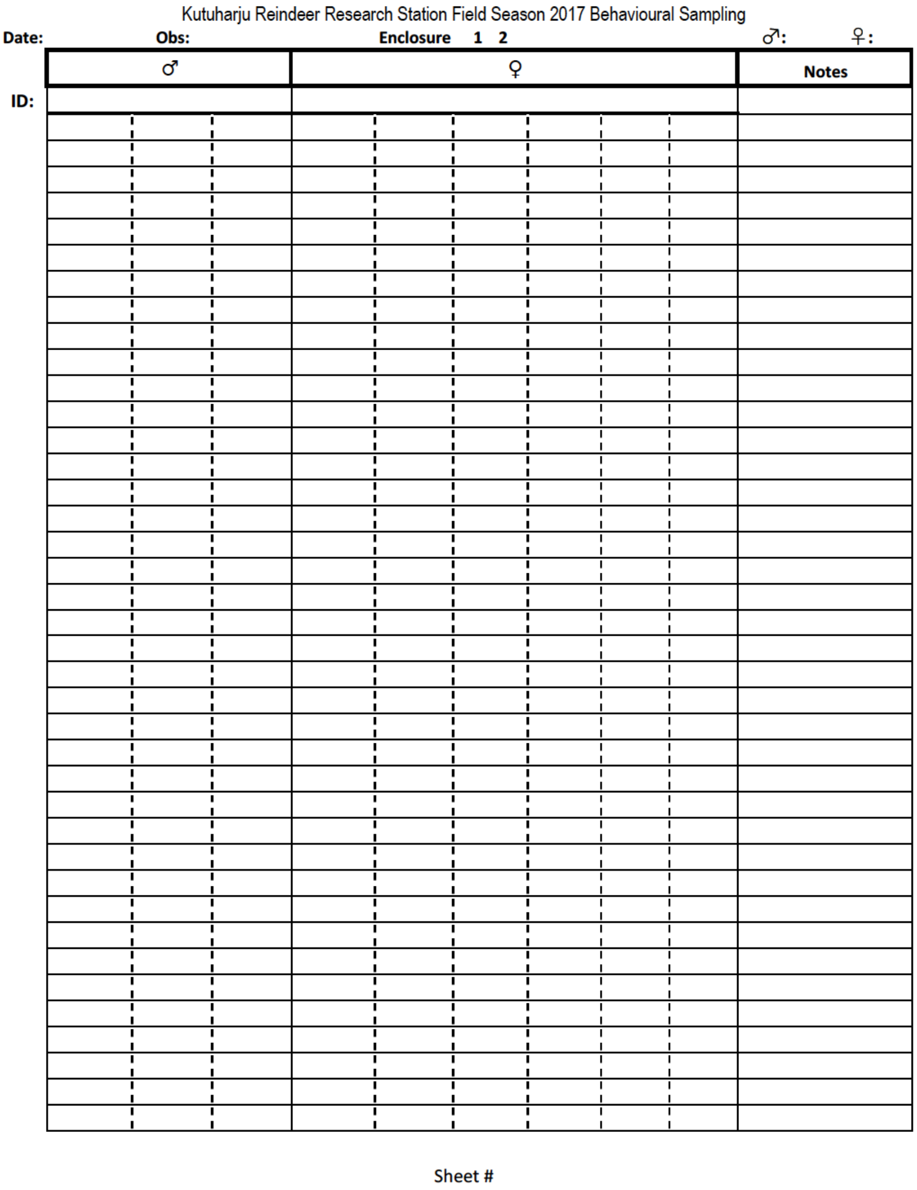


Trial 3 OSR 0.5	**PK 156**	**7764**	**PK 157**
PK 156	*****	**51**	**16**
7764	**0**	*****	**4**
PK 157	**0**	**10**	*****



Trial 3 OSR 1	**PK 159**	**PK 150**	**PK 148**
PK 159	*	25	28
PK 150	0	*	4
PK 148	0	0	*

Appendix C: Behavioural sampling form used for the collection of agonistic and courtship behaviours exhibited by male and female reindeer.



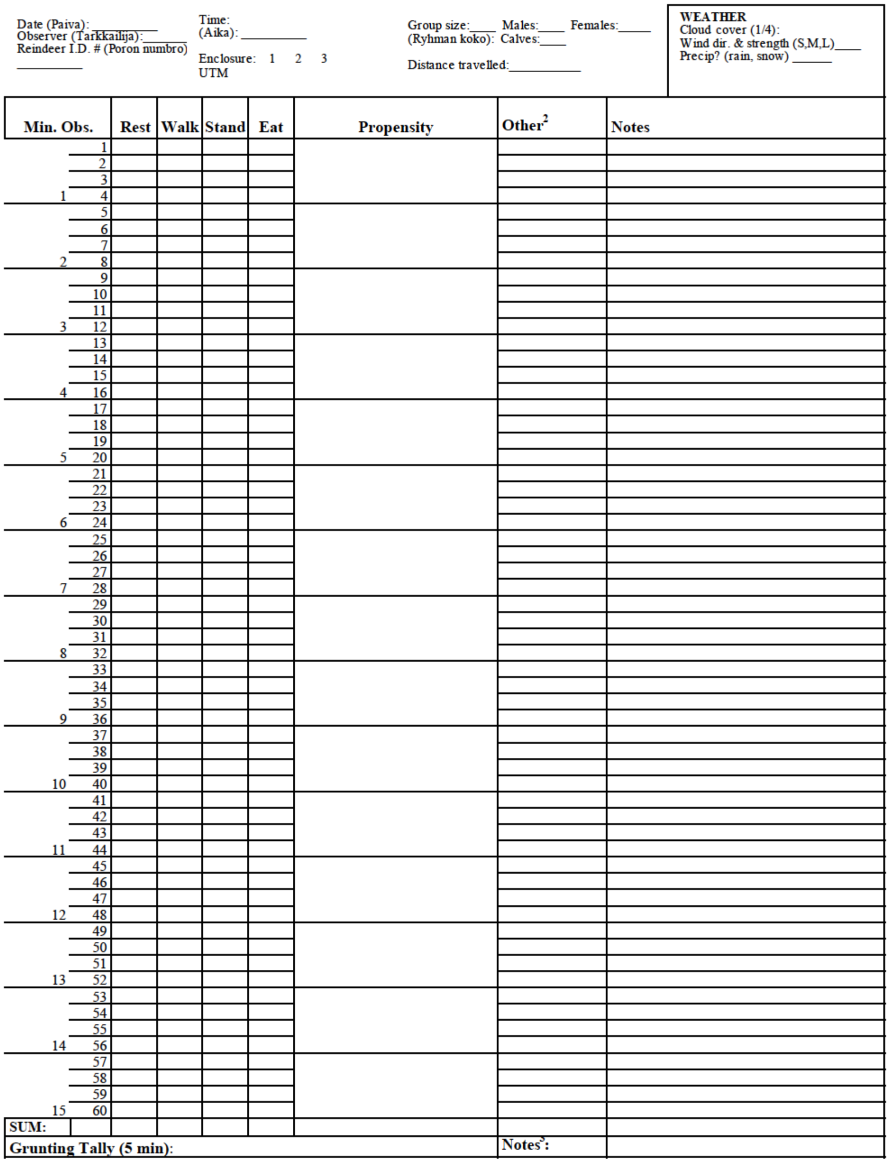
Kutuharju Reindeer Research Station Field Season 2017 Behavioural Sampling

Date: **Obs:** **Enclosure 1 2** ♂: ♀:

	♂			♀						**Notes**
ID:										

Sheet #

Appendix D: Focal sampling form used for the collection of behavioural data for the male reindeer activity budget.



Date (Paiva): __________
Observer (Tarkkailija):______
Reindeer I.D. # (Poron numbro)
____

Time:
(Aika): __________

Enclosure: 1 2 3
UTM

Group size:____ Males:____ Females:_____
(Ryhman koko): Calves:____

Distance travelled:__________

WEATHER
Cloud cover (1/4):
Wind dir. & strength (S,M,L)____
Precip? (rain, snow) ______

Min. Obs.		**Rest**	**Walk**	**Stand**	**Eat**	**Propensity**	**Other**[2]	**Notes**
	1							
	2							
	3							
1	4							
	5							
	6							
	7							
2	8							
	9							
	10							
	11							
3	12							
	13							
	14							
	15							
4	16							
	17							
	18							
	19							
5	20							
	21							
	22							
	23							
6	24							
	25							
	26							
	27							
7	28							
	29							
	30							
	31							
8	32							
	33							
	34							
	35							
9	36							
	37							
	38							
	39							
10	40							
	41							
	42							
	43							
11	44							
	45							
	46							
	47							
12	48							
	49							
	50							
	51							
13	52							
	53							
	54							
	55							
14	56							
	57							
	58							
	59							
15	60							
SUM:								
Grunting Tally (5 min):							**Notes**[3]**:**	

Appendix E: Characteristics of *Rangifer tarandus* individuals we used for our 2016 and 2017 field seasons at the Kutuharju Experimental Research Station in Kaamanen, Finland.

Reindeer ID	Sex	Age (Years)	Body weight (Kg)	Field Season	Notes
PK 151	M	2.5	95	2016	Replaced by PK 150 after trial 1 due to an infection
PK 152	M	2.5	105	2016	Replaced by Va J7764 after trial 1 due to injury
PK 156	M	2.5	105	2016	
PK 159	M	2.5	70	2016	April weigh in
PK 187	M	2.5	60	2016	April weigh in; Replaced by PK 148 after trial 1 because he jumped the fence
PK 157	M	2.5	96	2016	
PK 150	M	2.5	100	2016	
Va J7764	M	1.5	100	2016	
PK 148	M	2.5	68	2016	April weigh in
Va K233	M	1.5	76	2017	
Va K217	M	1.5	86	2017	
Va K230	M	1.5	86	2017	
Va K207	M	1.5	90	2017	
VaK261	M	1.5	97	2017	
7794	M	2.5	92	2017	
Ke72	F	3	77	2016	
Ke61	F	4	100	2016	
Ke74	F	3	84	2016	
NeKe35	F	5	95	2016	
Ke96	F	2	80	2016	
Ke80	F	3	84	2016	
NeKe25	F	6	100	2016	

Ke83	F	3	86	2016	
Ke85	F	2	87	2016	
Ke88	F	2	80	2016	
Ke87	F	2	85	2016	
Ru10	F	9	87	2016	
Ke93	F	2	74	2016	
Ke94	F	2	79	2016	
Vi11	F	7	91	2016	
Ke79	F	3	80	2016	
Ke92	F	2	85	2016	
Ke78	F	3	84	2016	
Vi2	F	8	94	2016	
Ru7	F	10	95	2016	
Vi15	F	7	99	2016	
NeKe34	F	5	90	2016	
Ke71	F	3	76	2016	
Ke75	F	3	74	2016	
Ke84	F	2	81	2016	
Ke86	F	2	84	2016	
Ke89	F	2	69	2016	
Ke93	F	3	65	2017	April weigh in
Ke76	F	4	71	2017	April weigh in
Ke74	F	4	77	2017	April weigh in
NeKe31	F	6	78	2017	April weigh in
Si6	F	2	68	2017	April weigh in
Si1	F	2	66	2017	April weigh in
Ke92	F	3	69	2017	April weigh in
Ke85	F	3	75	2017	March weigh in
NeKe34	F	6	77	2017	April weigh in
Ke96	F	3	70	2017	April weigh in
Ke87	F	3	83	2017	April weigh in

Ke80	F	4	70	2017	April weigh in
Ke63	F	5	76	2017	April weigh in
Si14	F	2	66	2017	April weigh in
Si9	F	2	63	2017	April weigh in
Ke84	F	4	69	2017	April weigh in
Ke70	F	4	74	2017	April weigh in
Ke61	F	5	87	2017	April weigh in
Ke66	F	5	90	2017	April weigh in
NeKe25	F	7	88	2017	April weigh in
Vi16	F	8	77	2017	April weigh in
Vi12	F	8	81	2017	April weigh in
Si17	F	2	68	2017	April weigh in
Si7	F	2	66	2017	April weigh in
NeKe45	F	6	79	2017	April weigh in
Si5	F	2	68	2017	April weigh in
Si3	F	2	60	2017	April weigh in