The Influence of Operational Sex Ratio on the Intensity of Competition in Reindeer (*Rangifer tarandus*) during Rut: An Experimental Approach

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ABSTRACT

The Influence of Operational Sex Ratio on the Intensity of Competition in Reindeer *(Rangifer tarandus)* during Rut: An Experimental Approach

Franco M. Alo

We examined how manipulating operational sex ratio (OSR: the ratio of reproductively active males to fertilizable females), could affect the intensity of competition in reindeer (*Rangifer tarandus*) using an experimental approach to test mating systems theory on the very first field study on large mammals of its kind. Study was conducted at the Kutuharju Reindeer Research Station where we had access to a herd of semi-domesticated reindeer. 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). Female reindeer were injected with 1 ml of estrumate prior to a trial to promote early and synchronized oestrous to assure competition among our 1.5-year-old males. We predicted that with increasing OSR, male-male aggression would increase and courtship behaviours would decrease, unless males adopted alternative mating tactics. Conversely, female-female aggression was predicted to decrease with increasing OSR. The propensity for males to act agonistically was predicted to increase with increasing OSR. Male-male rate of aggression did not differ between treatments. Female-female rate of aggression was found to decrease significantly with increasing OSR. Propensity to act agonistically was not significantly different between treatments. 1.5-year-old males may be too young and inexperienced to behave predictably. We conclude that the intensity of competition cannot be predicted at the group level based on OSR alone, though some trends emerged.

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INTRODUCTION

Competition for access to mates is quintessential in the pursuit to increase an individual's reproductive success. Of the various types of competition, probably the most common amongst mammals is contest competition **(Andersson & Iwasa 1996)**. Sexual selection, the evolution of adaptations that increase the mating success of certain individuals over others of the same sex and species, arises primarily from male-male competition and female mate choice **(Clutton-Brock 2007)**. The rate at which sexual traits evolve, depends largely on the outcome of competition and thus, the mating system observed has important consequences on the bearing of sexual selection. Polygyny for example, where males copulate with multiple females, promotes the potential presence of a given individual's genes being more prominent in the next generation due to high reproductive effort amongst males **(Clutton-Brock & McAuliffe 2009)**. Understanding the mechanisms of intra-specific competition involved in a certain species, can thus provide predictive power on the outcome of competition and approaches regarding its manipulation **(Andersson & Iwasa 1996)**.

Secondary sexual traits

It is theorized in **Darwin's (1871)** Descent of Man that mammalian males who exhibit ornamentation and high sexual dimorphism, compete intensely thereby designating them active strategists, while females tend to have a lower cost expenditure in this domain, giving the impression of being more passive. Darwin's theory then contrasts males as being mate limited, whilst females are resource limited and predator averse **(Bro-Jørgensen 2011)** thus explaining why males compete more intensely while females are responsible for mate choice. It is believed that females who have reduced or no ornaments and who compete less intensely, do so to maintain fecundity or parental investment as these traits are energy exhaustive **(Clutton-Brock 2009)**. These predictive frameworks direct the interactions that constitute mating systems.

Mating systems

Mating systems are numerous, and to a degree depend greatly on the spatial and temporal aggregation of many resources **(Clutton-Brock 1989)**. The degree of monopolization of those resources determines the variation in mating success of individuals **(Emlen & Oring 1977)**. Of the array of mating bonds possible (e.g. monogamy, polyandry, polygyny, and promiscuity), reindeer, our study species, belong to the 90% of mammals that are polygynous **(Clutton-Brock 1989)**. Though their mating behaviours may change in response to environmental and social fluxes, principals remains the same; males need to acquire females and females need to acquire resources in order to maximize their reproductive fitness **(Clutton-Brock 2007)**. Female aggregation in patches of high resource availability is thought to be at the forefront for the evolution of polygyny, where males can then access multiple females at one site **(Bebié & McElligott 2006)**, generating conflict between males resulting in competition for access to mates **(Clutton-Brock 2007)**.

Sexual selection

What is often not accounted for regardless of sex is how the operational sex ratio (OSR: ratio of reproductively active males to fertilizable females) of a population may affect the behaviour and interactions of those animals **(Emlen & Oring 1977; Reynolds 1996; Grant & Foam 2002)**. Quantifying sexual selection to predict an adaptive framework for mating systems has proven to be difficult for large mammals due to obvious logistical constraints surrounding their manipulation in natural or semi-natural settings **(Clutton-Brock & McComb 1993)**. Most papers deal primarily with males of taxa with small bodied animals in controlled environments **(Weir et al. 2011)**. By using an experimental approach, we hope to contribute to the understanding of mating system theories, which has been largely untested and which may prove powerful if trends are consistent across taxa. Moreover, few studies to date have paid considerable attention to female mating strategies **(Cotton et al. 2006)**, an aspect that we have incorporated in our design. Indeed, females play an important role in shaping sexual selection and may not be as passive as formerly thought **(Clutton-Brock & McComb 1993; Cotton et al. 2006; Bebié & McElligott 2006; Clutton-Brock & McAuliffe 2009; Pérez-González & Carranza 2011; Bro-Jørgensen 2011)**.

As OSR becomes increasingly biased towards a given sex, that sex will experience an increase in intraspecific competition **(Clutton-Brock & Vincent 1991; Andersson & Iwasa 1996; Lindenfors et al. 2007; Clutton-Brock 2007)** though an effect is not always detected, as discovered in the Alpine newt (*Triturus alpestis*)**(Denoël et al. 2005)**. **Jirotkul (1999b)** demonstrated that the strength of sexual selection in male Trinidadian guppies (*Poecilia reticulata*) decreased when population density increased, owing to reduced courtship behaviour at a controlled OSR and increased mate competition and mate choice due to higher encounter rates at high population densities. Manipulating population density, group size, and OSR have all led to numerous controversial evidence on their effects when considering the theory of sexual selection **(Kvarnemo & Ahnesjo 1996; Jirotkul 1999a; 1999b; Head et al. 2007; Klug et al. 2008; Sprenger et al. 2011)**. As such, we have kept male density and male age structure constant throughout the experiment, manipulating only the OSR. In recent years, it has been suggested in the literature that perhaps of equal interest is not only measuring the frequency of competitive behaviour, but rather addressing the more central question of when should individuals compete for mates. The propensity to act agonistically, i.e. the likelihood to engage in an agonistic behaviour given the opportunity during an encounter, measured as a rate, would more accurately reflect competition pressures and could be used to assess the strength of sexual selection across varying OSR **(de Jong et al. 2012)**. Given more opportunities to act agonistically or given a reduction in the ratio of females to males with increasing OSR, propensity for males to act agonistically should increase **(de Jong et al. 2012)**. This measure is therefore necessary to assess when individuals deem it necessary to act agonistically and take an opportunity to do so rather than invest time in other behaviours thereby reflecting the effect of varying competition pressures.

Reindeer, are sexually dimorphic like most other mammals **(Eisenberg 1981; Clutton-Brock 1989; McElligott et al. 2001; Lindenfors et al. 2007)**. As part of their elaborate social structure, male reproductive effort is directly related to female receptivity during the breeding season (rut) where few receptive females means few males reproducing successfully. Furthermore, as a result of varying competitive pressures, males may be forced to alter their mating tactics to suit a particular strategy. New male mating strategies (i.e. the number of approaches to acquiring a mate) may thus emerge to comply with varying population dynamics in order to insure maximum fitness is attained. As an example of a mating strategy, young subordinate reindeer males may stay with a female group and await the decline in sexual activity of a high-ranking male before attempting to mate **(Røed et al. 2002)**. This is also the case in bighorn sheep *Ovis canadensis* **(Pelletier et al. 2006)**, topi antelopes *Damaliscus lunatus* **(Bro-Jørgensen & Pangle 2010)**, fallow deer *Dama dama* **(Clutton-Brock & McComb 1993)**, and red deer *Cervus elaphus* **(Carranza et al. 1990)**. Most managed ungulate populations tend to be female-biased among adults **(Ginsberg & Milner Gulland 1994; Holand et al. 2006)**, thus having a low OSR implying greater mating opportunities for every individual male, at a cost. Studies have shown that adult male reindeer may lose up to 15% of their body mass during the rut **(Holand et al. 2006; Tennenhouse et al. 2011; Holand et al. 2012)**. This somatic cost is considerable and is the outcome of devoting a substantial amount of energy to reproductive effort and agonistic behaviours when competing for females **(Mysterud et al. 2003; Tennenhouse et al. 2011)**.

Costs associated to reproduction and competition

It is suggested that somatic and reproductive costs are a result of varying male rutting behaviour influenced by age **(Mysterud et al. 2003; Holand et al. 2006)**, density **(Sprenger et al. 2011)**, and group composition **(Tennenhouse et al. 2011)**. Group composition, the number of males present in a herd (mature or young), dictates both the intensity and competitive strategy used by old dominant male reindeer **(Tennenhouse et al. 2011)**. Unlike old dominant male reindeer, young males have higher capital breeding strategy constraints **(Kojola 1991)** meaning that unfavourable investment in early or late reproductive effort in light of females preferring larger adult males may simply be futile if unsuccessful **(Holand et al. 2006)**. The presence of young males alone leads to higher somatic costs and stress in female groups due to increased levels of harassment **(Clutton-Brock et al. 1996; Holand et al. 2006)**. Regardless of age, as the OSR becomes increasingly biased towards any particular sex, the most abundant sex will experience a higher intensity of competition and reduced courtship behaviours as the resource they are interested in is in limited supply **(Kvarnemo & Ahnesjo 1996)**. Until now, surprisingly few field studies have investigated the effect of OSR on competitive behaviour in the field while controlling for the aforementioned caveats **(Weir et al. 2011)**.

Agonistic behaviour

Agonistic behaviour may take many forms; from an energetically costly chase to a low intensity interaction such as sparring **(Tennenhouse et al. 2011)**. In reindeer, the variation in observed agonistic behaviour is dependent on social status, age, and experience **(Isvaran 2005; Tennenhouse et al. 2011)**. Harems (female aggregation in ungulates with one or more males) are typically controlled by the largest and highest ranking male individual **(Lindenfors et al. 2007)**. Older dominant males are more likely to win fights due to age and experience. Younger subordinate males are more prone to using harassment, forced mating, and even sneaking **(Røed et al. 2002; Isvaran 2005)** to avoid challenging superior competitors **(Pelletier et al. 2006)**. Female reindeer frequently aggregate into harems to decrease the level of harassment from such males though at the cost of increasing foraging competition between females **(L'Italien et al. 2012)**. **Holand et al. (2012)** describes reindeer males as having a mating strategy comprised of four main tactics decreasing in energetic cost accordingly, as well as potential gains: Dominant, Wannabe, Satellite, and Sneaker. Understanding how the presence of these mating tactics differs between OSR levels may shed light on the evolution of such tactics.

Objectives and predictions

Here using an experimental approach, we examine the effects of manipulating OSR on the strength of competition in reindeer, as manifested mainly by agonistic behaviour in 1.5-year-old males. To our knowledge, this is the first study to explore the effects of manipulating OSR on competitive behaviour in a field setting in a large mammal. Prior to reaching that conclusion, we performed a Web of Science query using the following words: "operational sex ratio" + "OSR" + "vertebrates" removing matches with "cells" + "human" due to the epidemiological nature of the results. This search revealed 50 matches of which 21 papers dealt with fish, the remaining dealing primarily with primates and amphibians and none on ungulates. As such, our aim is to determine if manipulating OSR on two levels will lead to variable strengths of competition in *R. tarandus*. We will test for the key predictions that (i) male-male aggression will increase with OSR whereas female-female aggression will decrease; (ii) courtship rate and duration will either decrease with OSR because of increased male-male competition or increase if males adopt alternative mating tactics (e.g. Sneaking); and (iii) propensity to act agonistically will increase with OSR.

METHODS

Reindeer and study area

A group of semi-domesticated reindeer was monitored during the rut from 14 September – 15 October 2015 at the Kutuharju Reindeer Research Station near Kaamanen, Finland (69˚N, 27°E). All individuals, including calves, were weighed to the nearest 0.1 kg and ear tagged. For this experiment, our reindeer were assigned to one of two experimental enclosures, at random. These areas are generally characterized by birch (*Betula spp.*) and Scots pine (*Pinus sylvestris*) forests amongst the many bogs and lakes covering vast topographically diverse plateaus **(L'Italien et al. 2012; Djaković et al. 2014)**.

We used ESRI (Environmental Systems Resource Institute)® ArcMap™ 10.0 to calculate percent dominant land cover type using the 'zonal histogram' tool to determine if there were significant differences between enclosures. Land cover imagery of the study area was acquired from Landsat 8 at a 30 m spatial resolution. A map of the enclosures was rendered using 152 coordinate data points collected from enclosure 1 and 197 coordinate data points collected from enclosure 2. Readings were taken every 16 ± 4 m using a Magellan Triton™ 300 GPS set to lat/long (deg.ddddd) coordinate system and the WGS84 map datum (Figure 1). Enclosure 1 (perimeter = 2.47 km, area = 0.41 km^2) was composed of 54 % treeless peatland and mire, 16 % mesic/submesic mountain birch, 12 % mesic/submesic young forest, 8 % mesic/submesic old growth and mature forest, 5 % water system, 4 % forested peatland and mire, and < 1 % nutrient-poor/dry old growth and mature forest. Enclosure 2 (perimeter = 3.03 km, area = 0.54 km^2) was composed of 42 % treeless peatland and mire, 17 % forest peatland and mire, 17 % mesic/submesic mountain birth, 14 % mesic/submesic young forest, 5 % mesic/submesic old growth and mature forest, 3 % water system, < 1 % nutrient-poor/dry old growth and mature forest, and < 1 % infrastructure area. Both enclosures were adjacent to each other and shared approximately 0.40 km of fencing. Though enclosures shared part of their Northern (enclosure 1) and Southern (enclosure 2) fence, no adequate solution was found to deter reindeer from obtaining any visual stimulus from conspecifics between treatments. Furthermore, this would not have inhibited any olfactory information transmission and thus total prevention of any type of interaction was not possible.

Experimental design

We manipulated OSR on two levels (3♂:6♀, 3♂:3♀ hereby referred to as 0.5 and 1 respectively) to assess its degree of influence on the intensity of intraspecific competition. In total, there were 6 male reindeer (age, 1.5-years-old; pre-rut mean weight ± SD = 75.5 ± 2.89 kg) and 36 female reindeer (age, range: 2.5 – 5.5-years-old; pre-trial mean weight ± SD = 79.4 ± 10.80 kg). Male age and density was kept constant so that any effect of treatment (OSR 0.5 or OSR 1) may be independent of these variables. The six 1.5-year-old males were fitted with very high frequency (VHF) collars so that they may be located within enclosures using radio telemetry. To assure independence of errors, the same 6 males were shuffled and chosen at random every trial, to be separated into two groups of 3 into either enclosure 1 or 2. In contrast, 9 females were replaced every day 0, corresponding with the day preceding the start of a new trial. On day 0 females were also weighed (i.e. pre-trial). Males on the other hand were weighed pre-rut (September 22nd), mid-rut (October 4th), and post-rut (October 19th) to evaluate any changes in mass gain/loss during trials (N = 4) corresponding to pre-study weight, mid-study weight, and post-study weight. Every trial consisted of 5 treatment days in both enclosures corresponding each to one OSR level (OSR 0.5 or OSR 1), with a total of 4 trials being performed over the length of the study.

We used systematic randomization with a Latin square design to vary the levels of OSR among our enclosures between trials. Our focus was on interspersion over strict randomization due solely to limitations of experimental design and lack of intra-trial replication with the aim to avoid getting segregated layouts. Though this introduces a small amount of bias, interspersion was expected to at least remove any potential for nondemonic intrusion and an effect of treatment which clearly would be false positive **(Hurlbert 1984)**. What is being replicated here is not the treatments, but the samples within single level of the treatment.

Ethics statement

In addition to data collection, animals were handled safely in accordance with the agreement from the Animal Ethics and Care certificate provided by Concordia University (AREC-30000303) and by the Finnish National Advisory Board on Research Ethics. Dr. Mauri

Nieminen, a senior Finnish reindeer research scientist, was granted permission by a local veterinarian in Kaamanen, Finland, to administer hormone injections to our experimental females, under professional supervision.

Estrumate injections

On day 0 of every trial, nine females were injected intramuscularly with 1 ml of estrumate® (cloprestenol sodium), an analogue of prostaglandin for cattle, to promote early oestrous. They were then separated into their respective treatments at random, and allowed one day to acclimate with the new group before any data collection ensued. During a reindeer's breeding season, behaviour normally progressively intensifies until peak rut (when most females are in oestrous)**(Holand et al. 2006; Body et al. 2014)**. Successful activation of estrumate meant that every trial was a miniaturized breeding season, motivating the males to not lose interest in the females thereby inducing rut-like behaviour. No experimental females were injected during trial 4 as their collection was unfortunately delayed during the season, putting them at risk of abortion if treated with estrumate while already having been copulated with. As a solution, we attempted to choose the youngest female reindeer for trial 4 as there exists a positive correlation between age of female reindeer and birth-weight of calves as related to time at conception **(Eloranta & Nieminen 1986)**. Younger females are more prone to being in oestrous and conceived with near the end of rut (trial 4). All experimental females were held in a paddock absent of males prior to their given trials to avoid copulation. Due to insufficient available forage in the paddock, experimental females were fed 2 kg individual $^{-1}$ day $^{-1}$ of supplementary dried commercial reindeer pellets (Poron-Herkku, Rehuraisio, Finland).

Behavioural measures

Group composition

Upon entering the enclosures, we recorded our arrival time and that of finding the first group. Our average search time was calculated across treatments and trials (mean ± 95% CI = 15.1 ± 2.5 min). We defined a group as being a cluster of individuals consisting of at least two individuals (male or female), 100 m from each other, which are synchronized in their activities (i.e. feeding/resting/walking/standing) and separated 100 m from another cluster of individuals **(Tennenhouse et al. 2011)**. With the fission-fusion dynamics of a group being very plastic, a new group composition was recorded any time individuals fused or parted for longer than 10 minutes. Following group compositions, throughout the day, groups were assessed for 1 of 4 possible mating tactics (see **(Holand et al. 2012)**). These counts were then transformed into presence/absence data. The total number of group compositions completed per day by any of the three observers was an indirect measure of how dispersed or clustered individuals were from each other in any given treatment. Group size and capacity (number of individuals present/ total number of individuals possible) were extracted from group composition data to determine how likely fission-fusion dynamics in a given OSR would change.

Propensity

As has been previously noted in the literature **(de Jong et al. 2012)**, measuring the frequency of agonistic interactions may not be the most representative when comparing the effect of OSR between two or more experimental treatment levels. Our interest was to quantify how often an opportunity to act agonistically was taken and whether changes in OSR would lead to changes in propensity. Propensity addresses the question, when should individuals compete for mates **(de Jong et al. 2012)**? We initially assessed through repeated observations a minimum radius for all individuals, in which an encounter would indisputably lead to an agonistic interaction between two reindeer. That distance was then slightly inflated as to capture more behaviour due to the uncertainty of using a standalone measurement that was to be fixed over time.

We used a radius of 2 meters for all males, and unfortunately, could not apply the same or any suitable distance to females as they were frequently found foraging within one body length of each other. If males entered each other's 2 meter radius and left without engaging in any agonistic behaviour, we scored that interaction a 0 for lack of engagement (i.e. the absence of an agonistic interaction given the opportunity). Conversely, an interaction that occurred between males inside this 2 meter radius was given a score of 1, signifying an agonistic interaction occurred. In this manner, number of engagements over total number of encounters (presence/absence of agonistic interactions within 2 meters between 2 individuals) resulted in our propensity measurement. An interval of 15 seconds was used to differentiate between any two given encounters, whereby the same individuals from a previous encounter needed to be more than 2 meters away from each other after the allotted time. If both individuals were within a 2 meter radius after the time interval and still no new agonistic interaction occurred, it was considered a new encounter. Propensity was measured during any of the two following sampling techniques.

Behavioural sampling

Behavioural sampling with continuous measuring was conducted in blocks of 15 minutes. Half the group or more had to be visible for sampling to ensue. Any missing individuals were excluded accordingly in relation to total time sampled. In this manner, we got an estimate of mean time every individual was sampled and pooled by sex and treatment level at the end of the day. Behaviours of interest were directly related to mating tactics and/or agonistic interactions such as but not limited to: follow, court, attempted copulation, chase, displace, fight, spar, head threats **(**see (**Tennenhouse et al. 2012)** for definitions**)**. Furthermore, related behaviours were grouped into two main categoriess to facilitate statistical analysis. These categories were agonistic (chases, displacements, spars, fights, head threats), and courtship (follow, attempted copulation, herd, court) behaviours. Bush thrashing was an individual display behaviour treated as such. Though initially part of the study, courtship duration was repeatedly difficult to measure despite the behaviour being ostentatious yet often extremely brief. As a substitute, a measure of courtship rate was calculated as the frequency of courtship behaviours divided by observation time. Where applicable, we documented interactions between individuals as either male-male (M:M), female-female (F:F), female-male (F:M) and male-female (M:F).

Focal sampling

Due to the nature of manipulating OSR and its potential impact on the intensity of competition, of relevance was observing if the male daily budget activity differed between treatment levels. Increased competition pressures might lead to a higher daily percentage of resting as a plausible corollary. Females are known to devote most of their time to foraging

(Uccheddu et al. 2015) and were largely of interest as to how active/rest times differed between treatments. No focal observations were performed on females allowing us to have a larger reported number of male observations (78 focals/ OSR corresponding to about 19.39 hours/OSR). We recorded whether a focal male was either feeding/resting/walking/standing/other every 15 seconds over a fifteen-minute block (Table 1). Any behaviour during focal or behavioural sampling that was of interest (despite not being part of the recording technique) was documented ad libitum (e.g. flehming, grunting).

Social hierarchy

All possible pairs of agonistic interactions were recorded and organized in a matrix with a winner and loser being identified. A loser was described as an individual being chased or displaced by another individual during an agonistic interaction. The individual doing the chasing or displacing was designated the winner. Improved Landau's index of linearity **(De Vries 1998)** was generated for each matrix and the rank of each individual was determined from the reordered matrices, all using Matman 1.1 for Windows **(Noldus 1998)**. Ranks were given values ranging 1 to 3, with 1 representing the least dominant male and 3 representing the most dominant male.

Inter observer reliability

Due to the multitude of sampling and recording techniques used in this experiment, we used data collected from simultaneous observations to investigate inter-observer reliability. In all three cases, we calculated the index of concordance for behavioural sampling measurements and the Pearson correlation coefficients for focal sampling measurements between the 3 pairs of observers **(Martin & Bateson 1993)**.

Statistical analysis

To examine differences between observed behavioural measures, we mainly used generalized linear mixed models (GLMM). A noteworthy exception was using a one sample paired t-test to assess if there were notable differences in mass gain of male reindeer individuals over the rut and a Welch two sample t-test to determine if there were differences between the numbers of mating tactics observed between treatments.

To determine the intensity of intra- and inter-sexual interactions, our response variables analyzed were: agonistic, bush thrashing, courtship behaviours from behavioural sampling, group composition and mating tactic, activity budget during focal sampling and propensity for both behavioural and focal sampling. Units of observation during statistical analysis were behavioural data pooled by day (n range = 40 – 160). Our GLMMs always had ‘treatment group’ as a random effect. Treatment group was defined as a group of reindeer under one OSR treatment in one trial. As such, we had 8 groups over 4 trials and were able to rule out any differences between groups due to non-independence of observations **(Thiele & Markussen 2012)**. This was of utmost importance since males were only shuffled between trials and not replaced. GLMMs were fit by maximum likelihood with Laplace Approximation. As we dealt predominantly with count data, those models had a z-transformed offset for average time spent observing day^{-1} to correct for scaling variable issues **(Bolker et al. 2009)**. Agonistic, bush thrashing, courtship, group composition, group ratio, group capacity and focal behaviours were all response variables fitted with a Poisson distribution with log link function. Mating tactics presence/absence, propensity and rest/active time response variables were fitted with a binomial distribution with logit link function. In case of over or under dispersion, GLMM was fitted with quasi-Poisson/binomial distribution.

To examine the relationship between response variables and determine if group means of a set of behaviours varied between treatments, we ran a multivariate analysis of variance (MANOVA). MANOVAs were done as a precursor to analyzing differences between individual behaviours if any. This was performed for focal sampling and behavioural sampling given the affinity for reindeer to perform only one behaviour not simultaneous with another. Irrespective of the response variables of interest, we always selected the most parsimonious model **(Burnham & Anderson 1998)**, computed by comparing the Akaike information criterion corrected (AICc) using the function ‘AICctab’ from the ‘bbmle’ package **(Ben Bolker & Team 2014)**. Fixed effects varied from model to model with the exception of OSR always being included. Note that for the results of all models, mean estimates are reported with their standard deviations and parameter estimates with their standard errors. In our agonistic model, intraspecific interactions were all compared against M:M with parameter estimates and standard errors stated for the interaction term. When evaluating the differences in bush thrashing rates between treatment levels, the interactions between OSR and sex were included to the quasi-Poisson model. The female biased treatment (OSR 0.5) was set as a control for all models since a group with 33% males most closely resembled the proportions you would find in managed reindeer herds **(Tennenhouse et al. 2011)**.

All analyses were performed in R version 3.2.2, R Core Team **(2015)**. The significance level was set to 0.05.

RESULTS

Male social hierarchy and body mass

The change in mass of males over the length of the study was not-significant (pre-mid: $t_{(5)} = -0.18$, $p = 0.86$; pre-post: $t_{(5)} = 0.66$, $p = 0.60$; mid-post: $t_{(5)} = 1.75$, $p = 0.14$). Independent of OSR, male social hierarchy was revealed to be highly linear in each group with a Landau's linearity index h' (corrected) of 1 (Table 2). Consistently in every trial, the two highest-ranking individuals were R25 and R29. They lost the most weight over 27 days (-0.185 kg/day and -0.074 kg/day, respectively) though this was non-significant when compared to all individuals change in mass (Table 3). By random chance alone, both these male reindeer (R25 and R29) were never present in the same treatment level.

Agonistic interactions

Male-male aggression did not increase with increasing OSR (estimate ± SE; $\beta = -0.02 \pm 0.35$, $p = 0.955$; Table 4), while female-female aggression did decrease significantly with increasing OSR ($\beta = -1.06 \pm 0.49$, $p = 0.034$; Figure 2). Female-male aggression was frequent at a rate significantly lower than male-male aggression independent of OSR ($\beta = -2.78 \pm 0.84$, $p = 0.001$; Figure 2). Among the agonistic behaviour category, not all behaviours were observed at equal rates (MANOVA: $F_{(1,158)} = 2.4$, $p = 0.011$). Female displacements were the most frequently observed agonistic interaction and differed significantly between OSR, being more prominent in the 0.5 treatment ($F_{(1,158)} = 5.03$, $p = 0.0263$; Table 5). Independent of OSR, rate of displacements and sparring were found to be significantly lower in female-male than male-male interactions independent of OSR ($\beta = -2.70 \pm 0.66$, $p < 0.001$; $\beta = -3.06 \pm 1.14$, $p = 0.009$). As would have been anticipated, male-male rate of sparring was also significantly higher than female-male rate of sparring independent of OSR ($\beta = -3.06 \pm 1.14$, $p = 0.009$). Female-male rate of head threats were significantly lower than male-male head threats, independent of OSR ($\beta = -2.15 \pm 0.66$, $p = 0.001$). Conversely, male-female head threat rate was significantly lower than female-female head threat rate independent of OSR ($\beta = -1.79 \pm 0.49$, $p < 0.001$).

Display behaviour

There was no difference in bush thrashing rates between OSR levels ($p = 0.505$). We did find a relationship between bush thrashing rates and OSR when the interaction between sexes and OSR was included in our model ($\beta = 1.17 \pm 0.37$, $p = 0.002$) where females in OSR 1 bush thrashed significantly less than females in OSR 0.5 ($\beta = -1.35 \pm 0.54$, $p = 0.015$; Figure 3). In OSR 0.5 alone, females bush thrashed significantly more than males ($\beta = 1.16 \pm 0.36$, $p = 0.006$).

Courting interactions

The rate of courtship behaviours did not differ between OSR levels ($p = 0.546$). Nonetheless, mean male attempted copulations were significantly lower in OSR 1 ($\beta = -2.06 \pm 0.92$, $p = 0.026$; Figure 4). Neither following, courting, or herding rates were significantly different between treatments (all $p > 0.05$).

Mating tactics and group compositions

Irrespective of the tactic observed, presence or absence of any discrete mating tactic documented was similar between OSR levels ($t_{(158)} = 0.81$, $p = 0.422$; Table 6). Wannabe, Satellite, and Sneaker mating tactics were, however, less present as compared to the Dominant mating tactic (Wannabe: $\beta = -2.71 \pm 0.80$, $p < 0.001$; Satellite: $\beta = -2.43 \pm 0.78$, $p = 0.001$; Sneaker: $\beta = -2.19 \pm 0.77$, $p = 0.004$; Figure 5), and this independent of OSR.

There was no difference in the number of group compositions completed daily by any of the observers in any given OSR ($p = 0.890$; mean ± SE = 2.53 ± 0.36). Nonetheless, in any given group composition, we found fewer females per group in OSR 1 compared to the number of females in OSR 0.5 ($\beta = -0.45 \pm 0.10$, $p = 0.004$). Granted that there was no significant difference in the number of individuals present per mating group independent of treatment, despite fewer total individuals in OSR 1 ($p = 0.081$), OSR 1 was significantly closer to harboring all potential individuals per group than OSR 0.5 ($\beta = 0.99 \pm 0.33$, $p = 0.030$).

Propensity

There was a significant difference in mean encounter rates between trials ($F_{(3,32)} = 4.79$, $p = 0.007$; Figure 6), though no significant difference existed between treatment levels ($p = 0.448$). As could be expected, there was a positive relationship between agonistic engagements and number of encounters ($\beta = 0.41 \pm 0.04$, $p < 0.001$; Figure 7). In spite of differences between individual components required to measure propensity, the willingness for males to act agonistically did not differ significantly between OSR levels ($p = 0.261$).

Focal sampling and rest/active periods

Upon comparing all focal behaviours independent of OSR, there were initially some clear contrasts (Figure 8). There were significant differences between the means of the five possible focal behaviours of interest ($t_{(779)} = 20.22$, $p < 0.001$; Figure 9) independent of OSR ($p = 0.179$) with eating being the most frequent recorded behaviour. In regards to active/rest periods of male and female reindeer, there was neither a significant difference between sexes, OSR, or an interaction of sex and OSR (all $p > 0.05$; Figure 10).

DISCUSSION

In the absence of older dominant males

Most ungulate studies have explored the effect of OSR on mixed-age groups with females known to prefer larger bodied males **(McElligott et al. 2001)**. Our 1.5-year-old males did not gain or lose a significant amount of mass during the experiment though they started at various weights. The two individuals that were repeatedly the most dominant (R25, R29) were not necessarily the heaviest or largest (Appendix A). With the absence of older dominant males, younger males could no longer rely on less risky mating tactics such as Sneaking **(Mysterud et al. 2003)**. To gain control over a harem and increase their reproductive success, they may have to shift to the Dominant mating tactic although their herding ability and display is not fully developed **(Holand et al. 2006)**. Female harassment by young males was still present though older males were absent in the group **(Uccheddu et al. 2015)**. The question is then, why haven't our males reacted as predicted with increasing OSR when all knowledge of competition in a polygynous species should point in the direction of increased male-male agonistic interactions **(Kvarnemo & Ahnesjo 1996)**? After all, the opportunity for sexual selection should be greatest amongst male-biased OSR where an increased variance between individuals leads to differing rates or reproductive success **(Mills & Reynolds 2003)**.

If male rank status was plastic, we presumed we could 'reset' male-male dynamics every trial, reinvigorating intraspecific competition through female estrumate injections. Regardless of the strong linearity (Appendix B) present in our social hierarchy, two individuals were consistently the most dominant throughout the trials. Rank status may not be as plastic as formerly thought and often the dominant individual in a group may be infrequently replaced by a subdominant. This is the case in mixed age groups, where there is greater variance in reproductive success **(McElligott et al. 2001)**. With males from one year to the next having larger body and antler sizes leaving the older larger male reindeer with a significant competitive advantage **(Lindenfors et al. 2007)**. It is for this reason that in a study with no varying age among males, we hypothesized that similar weights and body size would lead to fiercer competition for dominance as no individual had a clear competitive advantage.

In the presence of older dominant males, young reindeer males have been found to gain a significant amount of weight in comparison to their older counterparts as they typically avoid competing larger older males and instead feed and hedge their bets the following rut where a larger body size is favorable in asserting dominance **(Mysterud et al. 2003; Tennenhouse et al. 2011)**. Instead we found no significant change in body mass in our 1.5-year-old males during the entirety of the rut. Rather than increasing their energy allocation to feeding as previously mentioned, it may be possible that without older males, individuals spent more time in competitive behaviour though there was no difference between treatments. The absence of varying male age groups in a herd is highly unnatural among wild and even semi-domestic populations of reindeer **(L'Italien et al. 2012)**. It was necessary however to address one of the OSRs caveats, age structure.

Male mating tactics observed between treatments were not significantly different from one another, though 'Wannabe', 'Satellite', and 'Sneaking' were present at significantly lower values than the 'Dominant' mating tactic. The most abundant mating tactic observed was the 'Dominant' tactic as this above all else is the minimal requirement for having the opportunity to control a harem as stated by resource-defense theory **(Clutton-Brock 1989)**. With male density constant between treatment levels, we did not expect to see alternate mating tactics surpass the frequency of the observed Dominant tactic **(Isvaran 2005)**. Nonetheless, this is contrary to prediction (ii) where we had hoped to see an increase in alternate mating tactics in OSR 1 had there not been an increase in male-male agonistic interactions as expected. As we move from 'Dominant' to 'Wannabe' to 'Satellite' and 'Sneaker', there should be a decrease in the energy dedicated to such a tactic following a decrease in potential gain. In the face of higher competitive pressures, it may be more beneficial to adopt a tactic which is perhaps less beneficial in terms of potential direct access to mates yet has a lower energy expenditure.

In an attempt to relate mating tactics observed to group composition and the fission/fusion dynamics of such groups, there did not appear to be a trend in the number of individuals present in a group and the tactics observed independent of treatment. Groups independent of treatment were almost constantly at capacity thereby reflecting their native OSR. As previously suggested by **Body et al. (2014)**, this may be indicative of the tendency for females to decrease harassment by adhering to a group which has a high ranking male.

Additionally, as male reproductive fitness is strongly correlated to the stability of their groups, a group with fewer fission dynamics is ultimately beneficial to both male and female with the exception of lower ranking males which need to compete with the dominant male of the group or avoid them by adopting alternate mating tactics **(Body et al. 2014)**.

Whether a male chooses to avoid or engage in an agonistic bout can be determined through our measure of propensity. Though the propensity to behave agonistically was not different in either OSR over the length of the study with no support for prediction (iii), we did witness an interesting change in the encounter rates between trials and this was consistent across OSR levels. As the number of encounters increase somewhat linearly, there are greater opportunities to engage in an agonistic interaction between two males. As the onset of the rut progressed through time, encounter rates steadily diminished where they dipped at trial 3 before suddenly increasing in trial 4 to similar initial rates as trial 1. The data for trial 3 is interesting in that the dates, 5 – 9th October, agree with potential natural peak rut behaviour, or so we would conclude based on previous studies **(Body et al. 2014)** indicating that peak rut can last for approximately five days coinciding with the length of a single trial **(Pérez-González & Carranza 2011)**. The timing of the natural rut altogether is dependent on resource availability during the summer **(Djaković et al. 2012)**. Without an assessment of last summer's resources at the Kutuharju Reindeer Research Station, one can only speculate on the above statement. The use of estrumate was meant to counter behaviour that was phenologically distributed over the natural rut and instead provide miniaturized versions of a rut within trials; to be confirmed once we have received the paternity results of our experimental males. Female reindeer may only be sexually receptive for one to two days **(Ropstad 2000)**. Thus successful expression of estrumate in female reindeer would mean that males have a very sensitive time period to profit from receptive females.

Encounter rates dipping during trial 3 suggest that, at what was potentially peak natural rut, M:M agonistic interactions were at their lowest implying that the dominant male who tried to repeatedly court, herd, follow, and copulate with females was practically unchallenged. Alternatively, it is possible that our 2 meter male radius used for our propensity measurement was too small to capture all behaviours. At peak rut, dominant males should act maximally to defend their resource (females) by engaging in costly agonistic behaviour such as chases, displacements, and fights **(Tennenhouse et al. 2011)**. These behaviours might be engaged at distances greater than 2 meters in which case our sampling methods would have failed to capture said behaviour. If this is so, it would insinuate that the territory size of males can fluctuate during the rut following a Gaussian distribution where at peak rut dominant males are less likely to allow subdominants to approach them at risk of being overthrown and losing their resources. We thereby recognize **deJong (2012)** in affirming that propensity is an indicator of the intensity of competition by assessing the number of opportunities taken to act agonistically between individuals. On the other hand we can now delve into the topic of personality in subdominants and dominant males based on propensity alone where a higher propensity score may indicate risk prone individuals and a lower propensity score might indicate risk averse individuals **(Strong 2015)**.

Unable to control for any of the OSR caveats with females (age, density, group composition), it remained that we had significant evidence to support that F:F agonistic behaviour decreased with increasing OSR **(Kvarnemo & Ahnesjo 1996)**. Though **Kvanermo & Ahnesjo (1996)** used a different calculation for OSR (number of of males/number of males + females), increasing OSR still signifies a reduction in both the intensity of competition between females and female mate choice. Female mate choice in itself is difficult to prove. Are the females being more aggressive towards each other to attract the dominant male or are they simply defending and claiming a food resource patch? This study does reinforce the female foraging competition hypothesis where an increase in the number of reindeer females per group (i.e. increased density) leads to more time spent doing other related social behaviours **(Uccheddu et al. 2015)** as supported by the fact that F:F rates of aggression (i.e. disturbance) and bush thrashing in OSR 0.5 were significantly higher than F:F rates of aggression in OSR 1. It has been repeatedly suggested that females do play an important role in mating dynamics **(Andersson & Iwasa 1996; Jirotkul 1999a; Young et al. 2010)**, information that should bear more weight on experimental research on the study of mating systems though the literature is inherently male biased.

It must not be forgotten that these 1.5-year-old reindeer males have recently become sexually mature and are in their first rut with no prior experience on how to engage in M:M agonistic interactions **(Tennenhouse et al. 2012)**, or courting for that matter and even considered immature **(L'Italien et al. 2012)**. There was not a single account of mate guarding or scent marking (male who urinates on hind legs to assert dominance) and a very late emergence of flehmen (when male expose their vomeronasal organ to air as a means of courting) which are all behaviours normally present in older dominant males **(Isvaran 2005)**. Regardless of potential immaturity and inexperience, we propose that the lowest rate of agonistic interactions observed, between F:M, is caused by the necessity for females to remain sexually receptive and avoid deterring a potential mate, even if that mate is a young male.

Seemingly contrary to predictions from theory **(Emlen & Oring 1977; Kvarnemo & Ahnesjo 1996)**, we found that males courted more in the female-biased OSR. This study adds to a growing body of evidence that the frequencies of different competitive behaviours do not react uniformly to a change in OSR or density. It does however reinforce the concept that males who compete more intensely are then at a better advantage to court and copulate though prediction (ii) was not supported in this respect. Bush thrashing, a poorly understood display behaviour, was present at the highest rates in OSR 0.5 by females. Reiterating, females in OSR 0.5 also had higher rates of aggression than females from OSR 1. It is therefore possible that subdominant females in OSR 0.5 were actively bush thrashing to attract males. It is unlikely that females were bush thrashing simply to remove the velvet from their antlers as there was no difference in bush thrashing rates between trials with velvet shedding most often observed during early rut **(Adams et al. 2001)**. We also observed that upon bush thrashing, usually a pine sapling, reindeer would lick the sap from the damaged bark as a way to potentially ingest a nutrient otherwise not present in their main food source. This type of behaviour was so predictable that a certain height of sapling was as expected almost always bush thrashed by reindeer. Bush thrashing may therefore serve as a public display of attention for females, while **Adams et al. (2001)** show that males may do this as a form of scent marking in synchrony with oestrous.

Less predictable was the rate and frequency of attempted copulations. In total there were 28 attempted copulations recorded, including the ad libitum data. Based on an average of 7 hours a day spent in enclosures and a total of 118.9 hours of behavioural sampling completed between observers, the frequency of witnessing an attempted copulation was approximately 1 for every 4.25 hours of observation time or 0.2 attempted copulations/hour. This low rate may be due to the fact that during what is recorded as cervid peak rut hours, 1600 – 1930 hours, we had a tendency to be absent in the second half of that period due to the distance from the research station the enclosures were located and a quick occurring dusk **(Carranza et al. 1990)**. Specifically, this poses a problem as with 36 females, we have less than the number of attempted copulations required to confidently say that every female was potentially copulated with. In addition, most attempted copulations observed were focused on a select few females per trial as if certain females would be more attractive to males than others.

Due to females spending as past research mentions, roughly 75% of their time feeding **(Djaković et al. 2014)**, the motivation behind focal sampling was to determine what males were doing on average with their time. With no significant trend between OSR levels, it was found that males foraged on average 63% of the time. This value is believed to be lower than if our experimental males were among a mixed age group where young males generally avoid confrontation with larger dominant males **(Tennenhouse et al. 2012)**, potentially indicating that young male and all aged female foraging rates would be similar. The fact that it is lower is indicative of the increased agonistic interactions we were able to instil by manipulating OSR with 1.5-year-old male reindeers whereby they shifted from a less costly/risky mating tactic of Sneaking, to asserting themselves and attempting to overthrow a dominant individual **(Mysterud et al. 2003)**. However, with such a high percentage of eating as a substitute to engaging in other behaviours more prone to increasing ones reproductive success (agonistic/courtship), the conclusion must be drawn that 1.5-year-old males as previously noted are somewhat immature, inexperienced, and have not yet fully developed strong mating tactics **(Pérez-González & Carranza 2011; Holand et al. 2012; Tennenhouse et al. 2012)**. In regards to how the time of male behaviour was partitioned during focal sampling, our interests in activity budget also led us to analyze if the highly competitive nature in one OSR over the other meant more time resting. It was found that independent of OSR, males and females rested, on average, the same amount of time. Though statistically non-significant, females rested slightly longer than males and this independently of OSR. Biologically, the inferences we can deduct are that females as the limiting resource during the rut, control the activity of a harem **(Bro-Jørgensen 2011)**. A male who rests before a female is at a disadvantage if a mating opportunity presents itself and should thereby remain active until all females have ceased to forage and rest. Even then, males would sometimes harass females to get up and attempt to copulate.

In light of synthesizing results and addressing our predictions, there was support to show that (i) F:F agonistic interactions decreased with increasing OSR but no support to show that M:M agonistic interactions increased with OSR. We acknowledge that our number of replicates were few and that this may have underpowered our statistical inferences. Without statistically significant differences in courtship rates between OSR levels, we had no support for prediction (ii) which suggested courtship rate would either decrease with OSR because of increased M:M competition or increase if males adopted alternative mating tactics (e.g. Sneaking). No alternative mating tactics were adopted at significant rates, with Dominant being the most frequent mating tactic in both OSRs. Finally, (iii) propensity to act agonistically did not increase with OSR and was therefore not a supported prediction. More care should be given when choosing an individual radius to assess opportunity. As we have experienced based on this study, underrepresenting a measurement might mean a lack of evidence to detect an effect between treatments.

With future work aimed at replicating this study with 2.5-year-old reindeer males, it will be interesting to see if our few emerging trends persist, or if age as we might think, can really be a factor in how male reindeer interact in the face of manipulating OSR.

REFERENCES

Adams, C. A., R. T. Bowyer, J. E. Rowell, W. E. Hauer, and J. A. Jenks. 2001. Scent marking by male caribou: an experimental test of rubbing behavior. Rangifer **21**:21–27.

Andersson, M., and Y. Iwasa. 1996. Sexual selection. Trends in Ecology & Evolution **11**:53–58.

Bebié, N., and A. G. McElligott. 2006. Female aggression in red deer: Does it indicate competition for mates? Mammalian Biology - Zeitschrift für Säugetierkunde **71**:347–355.

Body, G., R. B. Weladji, Ø. Holand, and M. Nieminen. 2014. Highly Competitive Reindeer Males Control Female Behavior during the Rut. PloS one **9**:e95618.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127–135.

Bolker, B., and R. D. C. Team. 2014. bbmle: Tools for general maximum likelihood estimation. http://CRAN.R-project.org/package=bbmle.

Bro-Jørgensen, J. 2011. Intra-and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. Evolutionary Biology **38**:28–41. Springer.

Bro-Jørgensen, J., and W. M. Pangle. 2010. Male Topi Antelopes Alarm Snort Deceptively to Retain Females for Mating. The American Naturalist **176**:E33–E39.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach: 60-64.

Carranza, J., F. Alvarez, and T. Redondo. 1990. Territoriality as a mating strategy in red deer. Animal Behaviour **40**:79–88. Elsevier.

Clutton-Brock, T. 2007. Sexual Selection in Males and Females. Science **318**:1882–1885.

Clutton-Brock, T. 2009. Sexual selection in females. Animal Behaviour **77**:3–11.

Clutton-Brock, T. H. 1989. Mammalian mating systems. Proceedings of the Royal Society of London. Series B, Containing papers of a Biological character. Royal Society (Great Britain) **236**:339–372.

Clutton-Brock, T. H., and A. C. Vincent. 1991. Sexual selection and the potential reproductive rates of males and females. Nature **351**:58–60.

Clutton-Brock, T. H., K. E. McComb, and J. C. Deutsch. 1996. Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. Behavioral Ecology **7**:373–378.

Clutton-Brock, T., and K. McAuliffe. 2009. Female Mate Choice in Mammals. The Quarterly review of biology **84**:3–27.

Clutton-Brock, T., and K. McComb. 1993. Experimental tests of copying and mate choice in fallow deer (*Dama dama*). Behavioral Ecology **4**:191–193.

Cotton, S., J. Small, and A. Pomiankowski. 2006. Sexual Selection and Condition-Dependent Mate Preferences. Current Biology **16**:R755–R765.

Darwin, C. 1871. Sexual selection and the descent of man. Murray, London.

de Jong, K., E. Forsgren, H. Sandvik, and T. Amundsen. 2012. Measuring mating competition correctly: available evidence supports operational sex ratio theory. Behavioral Ecology **23**:1170–1177.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour **55**:827–843.

Denoël, M., M.-P. Hector, and P. Poncin. 2005. Courtship behavior in the Alpine newt Triturus alpestris at two different densities of males. Herpetologica **61**:373–379.

Djaković, N., Ø. Holand, A. L. Hovland, K. H. Røed, R. B. Weladji, E. Fjeldstad, and M. Nieminen. 2012. Association patterns and kinship in female reindeer (Rangifer tarandus) during rut. Acta Ethologica **15**:165–171 .

Djaković, N., Ø. Holand, A. L. Hovland, R. B. Weladji, K. H. Røed, and M. Nieminen. 2014. Effects of males' presence on female behaviour during the rut. Ethology Ecology & Evolution **27**:148–160.

Eloranta, E., and M. Nieminen. 1986. Calving of the experimental reindeer herd in Kaamanen during 1970 - 85. Rangifer **6**:115–121.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science **197**:215–223.

Ginsberg, J. R., and E. J. Milner Gulland. 1994. Sex-Biased Harvesting and Population Dynamics in Ungulates: Implications for Conservation and Sustainable Use. Conservation Biology **8**:157–166.

Grant, J. W. A., and P. E. Foam. 2002. Effect of operational sex ratio on female-female versus male--male competitive aggression. Canadian Journal of Zoology **80**:2242–2246.

Head, M. L., A. K. Lindholm, and R. Brooks. 2007. Operational sex ratio and density do not affect directional selection on male sexual ornaments and behavior. Evolution **62**:135–144.

Holand, Ø., L. L'Italien, R. B. Weladji, N. Djaković, K. Røed, A. L. Hovland, and M. Nieminen. 2012. Shit happens–a glimpse into males' mating tactics in a polygynous ungulate-the reindeer. Rangifer **32**:65–72.

Holand, Ø., R. B. Weladji, K. H. Røed, H. Gjøstein, J. Kumpula, J. M. Gaillard, M. E. Smith, and M. Nieminen. 2006. Male age structure influences females' mass change during rut in a polygynous ungulate: the reindeer (Rangifer tarandus). Behavioral Ecology and Sociobiology **59**:682–688.

Hurlbert, S. H. 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs **54**:187–211. Ecological Society of America.

Isvaran, K. 2005. Variation in male mating behaviour within ungulate populations: patterns and processes. Current Science **89**:1192–1199.

Jirotkul. 1999a. Operational sex ratio influences female preference and male-male competition in guppies. Animal Behaviour **58**:8–8.

Jirotkul. 1999b. Population density influences male-male competition in guppies. Animal Behaviour **58**:7–7.

Klug, H., C. I. Kontax, S. Annis, and N. Vasudevan. 2008. Operational sex ratio affects nest tending and aggression in male flagfish Jordanella floridae Goode & Bean. Journal of Fish Biology **72**:1295–1305.

Kojola, I. 1991. Influence of age on the reproductive effort of male reindeer. Journal of Mammalogy **72**:208–210.

Kvarnemo, C., and I. Ahnesjo. 1996. The dynamics of operational sex ratios and competition for mates. Trends in Ecology & Evolution **11**:404–408.

Lindenfors, P., J. L. Gittleman, and K. E. Jones. 2007. Sexual size dimorphism in mammals. Sex, size and gender roles: evolutionary studies of sexual size dimorphism:16–26. Oxford University Press Inc. New York.

L'Italien, L., R. B. Weladji, Ø. Holand, K. H. Røed, M. Nieminen, and S. D. Côté. 2012. Mating Group Size and Stability in Reindeer Rangifer tarandus: The Effects of Male Characteristics, Sex Ratio and Male Age Structure. Ethology **118**:783–792.

Martin, P., and P. P. G. Bateson. 1993. Measuring behaviour: an introductory guide. Cambridge University Press.

McElligott, A. G., M. P. Gammell, H. C. Harty, D. R. Paini, D. T. Murphy, J. T. Walsh, and T. J. Hayden. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? Behavioral Ecology and Sociobiology **49**:266–272.

Mills, S. C., and J. D. Reynolds. 2003. Operational sex ratio and alternative reproductive behaviours in the European bitterling, Rhodeus sericeus. Behavioral Ecology and Sociobiology **54**:98–104.

Mysterud, A., Ø. Holand, K. H. Røed, H. Gjøstein, J. Kumpula, and M. Nieminen. 2003. Effects of age, density and sex ratio on reproductive effort in male reindeer (Rangifer tarandus). Journal of Zoology **261**:341–344.

Noldus Information Technology. 1998. Matman reference manual. Version 1.1 for Windows. Wageningen, The Netherlands.

Pelletier, F., J. T. Hogg, and M. Festa-Bianchet. 2006. Male mating effort in a polygynous ungulate. Behavioral Ecology and Sociobiology **60**:645–654.

Pérez-González, J., and J. Carranza. 2011. Female aggregation interacts with population structure to influence the degree of polygyny in red deer. Animal Behaviour **82**:957–970.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Reynolds, J. D. 1996. Animal breeding systems. Trends in Ecology & Evolution **11**:68–72.

Ropstad, E. 2000. Reproduction in female reindeer. Animal Reproduction Science **60-61**:561–570.

Røed, K. H., Ø. Holand, M. E. Smith, H. Gjøstein, J. Kumpula, and M. Nieminen. 2002. Reproductive success in reindeer males in a herd with varying sex ratio. Molecular Ecology **11**:1239–1243.

Sprenger, D., R. Lange, and N. Anthes. 2011. Population density and group size effects on reproductive behavior in a simultaneous hermaphrodite. BMC Evolutionary Biology **11**:107.

Strong, J. S. 2015. Investigation of personality in subdominant male reindeer (Rangifer tarandus) and its relation to somatic cost and reproductive success [MSc thesis]. Concordia University, Montreal.

Tennenhouse, E. M., R. B. Weladji, Ø. Holand, and M. Nieminen. 2012. Timing of reproductive effort differs between young and old dominant male reindeer. Annales Zoologici Fennici **49**:152–160.

Tennenhouse, E. M., R. B. Weladji, Ø. Holand, K. H. Røed, and M. Nieminen. 2011. Mating group composition influences somatic costs and activity in rutting dominant male reindeer (Rangifer tarandus). Behavioral Ecology and Sociobiology **65**:287–295.

Thiele, J., and B. Markussen. 2012. Potential of GLMM in modelling invasive spread. CAB Reviews **7**:1–10.

Uccheddu, S., G. Body, R. B. Weladji, Ø. Holand, and M. Nieminen. 2015. Foraging competition in larger groups overrides harassment avoidance benefits in female reindeer (Rangifer tarandus). Oecologia **3**:711–718.

Weir, L. K., J. W. A. Grant, and J. A. Hutchings. 2011. The Influence of Operational Sex Ratio on the Intensity of Competition for Mates. The American Naturalist **177**:167–176.

Young, M. J., L. W. Simmons, and J. P. Evans. 2010. Pre- and post-mating sexual selection both favor large males in a rainbowfish. Behavioral Ecology and Sociobiology **64**:915–925.

TABLES

Table 1: Mean male activity budget across trials (N = 4) for focal observations (15 min = 60 instanteous sampling events every 15 s).

Activity	Mean frequency (out of 60)	%
Rest	3	5.00
Walk	11	18.33
Stand	5	8.33
Eat	38	63.33
Other	3	5.00

Table 2: Male social hierarchy relationships based on matrix total represented by total number of agonistic interactions in a given trial at a given OSR. All Chi-square values for the individual matrices were undefined with p-values > 0.05.

Trial	OSR	Matrix total	Directional consistency index
1	0.5	68	0.765
1	1	143	0.874
2	0.5	78	0.974
2	1	145	0.931
3	0.5	98	1.000
3	1	88	0.977
4	0.5	210	0.981
4	1	58	0.931

Table 3: Male reindeer mass rate of change over 27 days encompassing pre-rut, mid-rut, and post-rut periods designated here as pre-study, mid-study, and post-study.

Reindeer ID	Rank*	Pre-study mass (kg)	Mid-study mass (kg)	Post-study mass (kg)	Change in mass (27 days, kg/day)
R25	6	75	73	70	-0.185
R29	5	79	77	77	-0.074
R24	4	71	75	75	0.148
R22	3	78	79	78	0.000
R01	2	74	74	73	-0.037
R19	1	76	76	76	0.000

* Rank 6 is designated to the most dominant individual and subsequently dominance decreases with rank with 1 being the lowest ranking individual.

Table 4: Parameter estimates ± standard errors (SE) for agonistic interactions. All interactions (noted by “int”) are in contrast to OSR 0.5 and M:M. Bold p-values indicate statistical significance (α = 0.05).

Parameter	**Estimate ± SE**	**DF**	**t-value**	**p-value**
OSR 1	-0.021 ± 0.348	6	-0.059	0.955
int F:F	0.0345 ± 0.283	146	0.122	0.903
int F:M	-2.777 ± 0.839	146	-3.311	**0.001**
int M:F	-0.473 ± 0.323	146	-1.464	0.145
OSR 1 x int F:F	-1.058 ± 0.495	146	-2.140	**0.034**
OSR 1 x int F:M	0.452 ± 1.093	146	0.413	0.679
OSR 1 x int M:F	-0.428 ± 0.502	146	-0.853	0.395

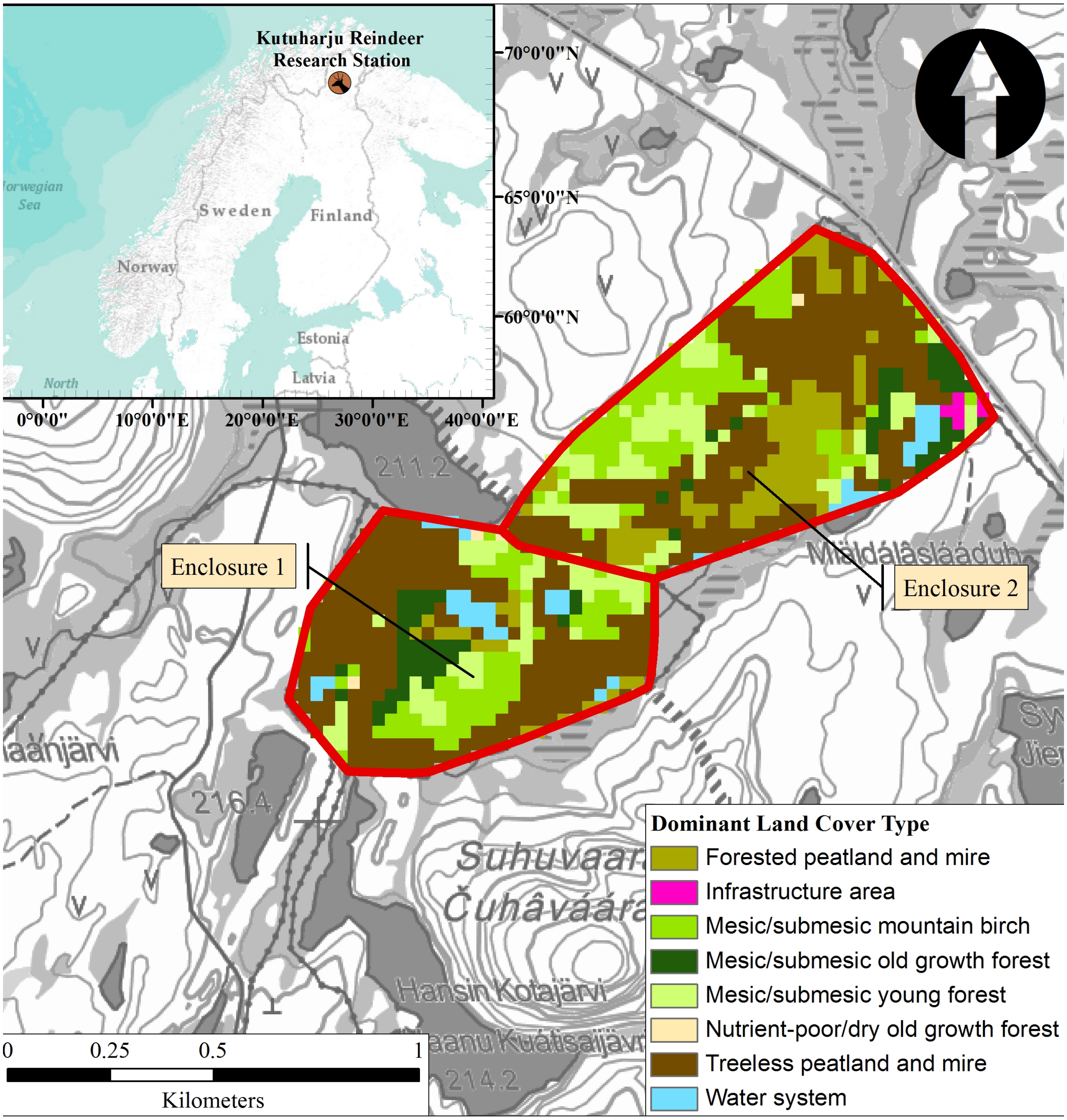
Table 5: Agonistic interactions observed between treatments (OSR 0.5 and 1) and between four possible sex:sex interaction types over 4 trials. Values reported as frequencies.

OSR	Interaction	Agonistic behaviours				
		Displacements	Chases	Sparrs	Fights	Head threats
0.5	M:M	214	32	111	4	54
1	M:M	178	44	90	11	67
0.5	F:F	251	7	9	0	149
1	F:F	90	3	1	1	43
0.5	F:M	14	0	8	0	6
1	F:M	20	1	4	0	14
0.5	M:F	191	36	8	0	26
1	M:F	124	15	5	0	17

Table 6: Comparing presence/absence (p/a) scores of male mating tactics observed each day in a mating group in every OSR level. A value of 0 indicates the absence of a mating tactic and a value of 1 indicates the presence of a mating tactic.

OSR	p/a	Tactic				∑
		Dominant	Wannabe	Satellite	Sneaker	
0.5	0	4	15	14	13	46
1	0	6	13	13	19	51
0.5	1	16	5	6	7	34
1	1	14	7	7	1	29

FIGURES



Source: Landsat-5 TM 5.7.2005 & Aster-Terra 30.7.2006.

Figure 1: Map of enclosures and their constituting dominant land cover types at the Kutuharju Reindeer Research Station. Red lines represent the boundaries of each enclosure with enclosure 1 and 2 sharing ~ 0.40 km of fencing.

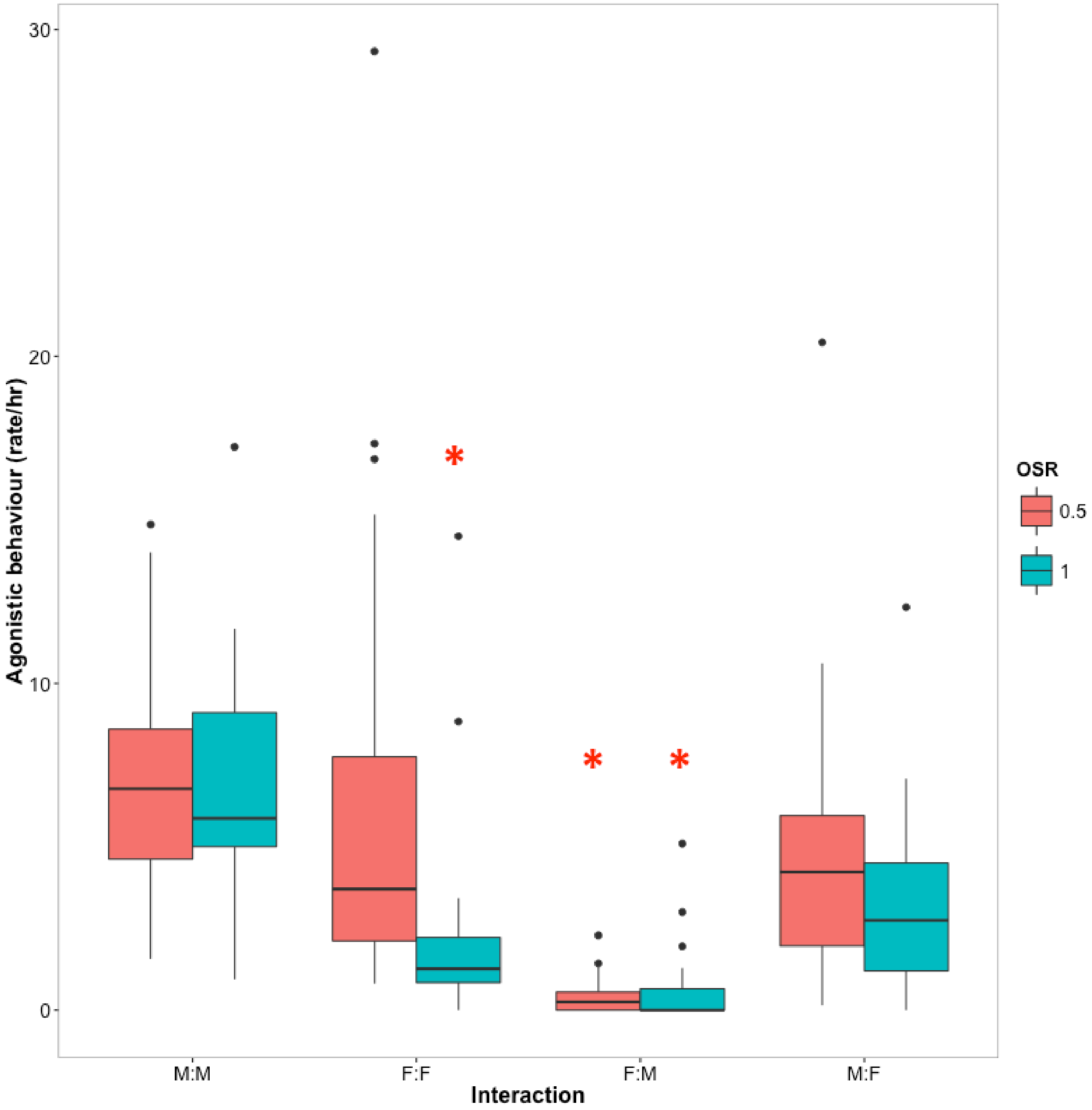


Figure 2: Daily mean rate of agonistic behaviours based on four possible interactions (M:M, F:F, F:M, M:F) between OSR levels (0.5, 1). Closed black circles represent outliers while the red asterisks are above significant interactions with p-values < 0.05.

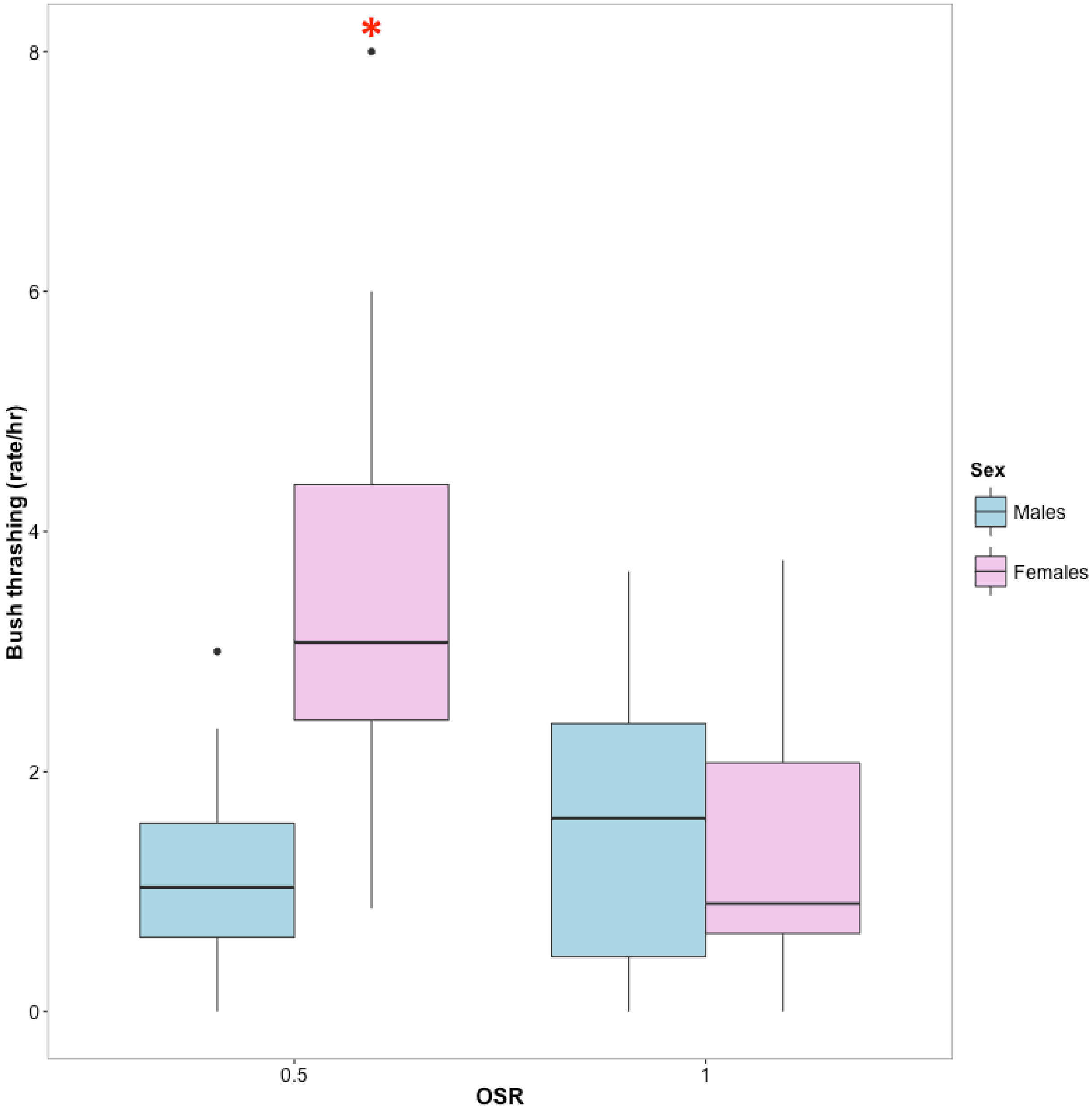


Figure 3: Hourly mean rate of bush thrashing based on interactions between OSR:Sex. Closed black circles represent outliers while the red asterisks are above significant interactions with p-values < 0.05.

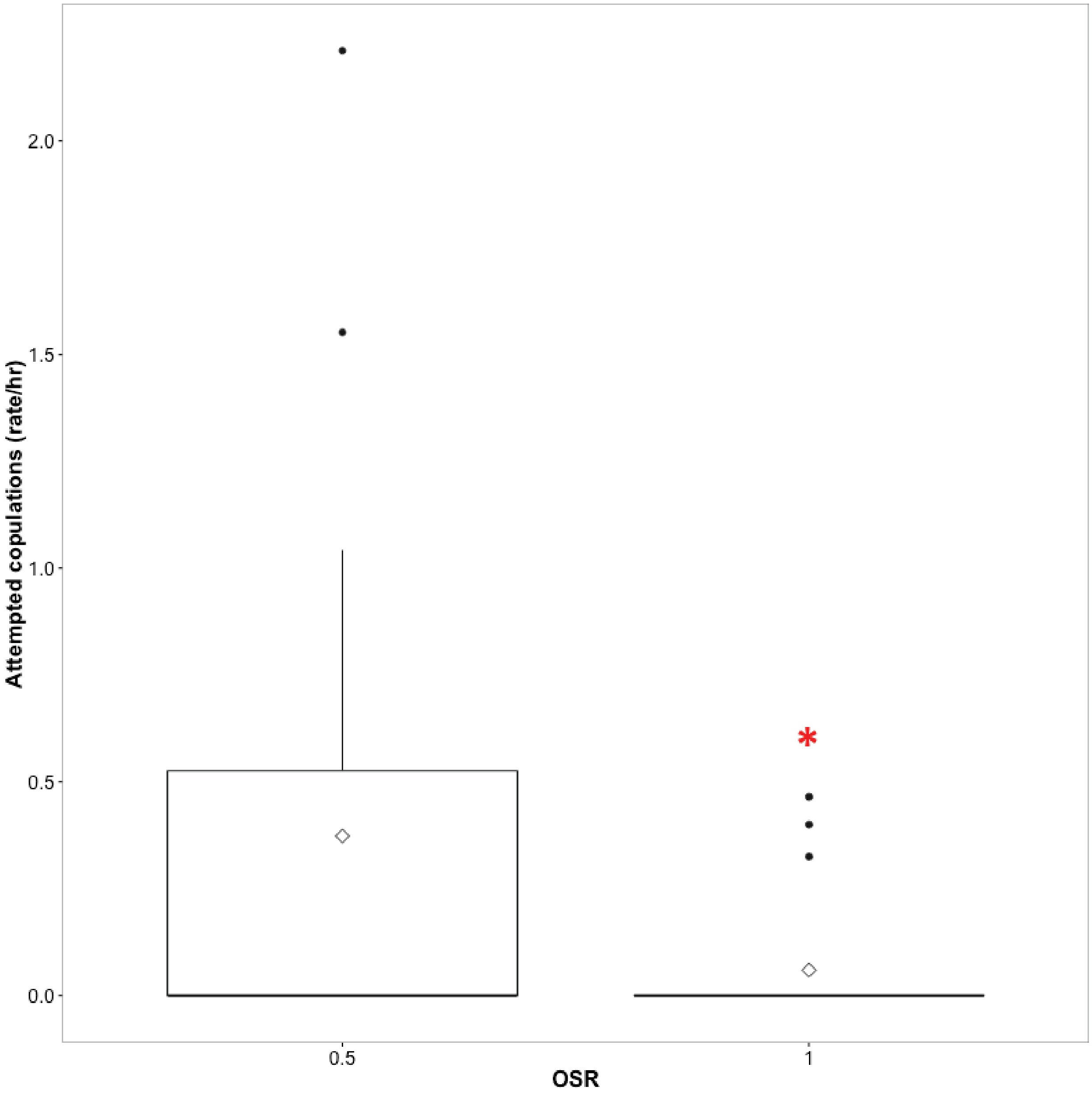


Figure 4: Hourly mean rate of attempted copulations between OSR. Closed black circles represent outliers while open diamonds represent group means. The red asterisks are above significant interactions with p-values < 0.05.

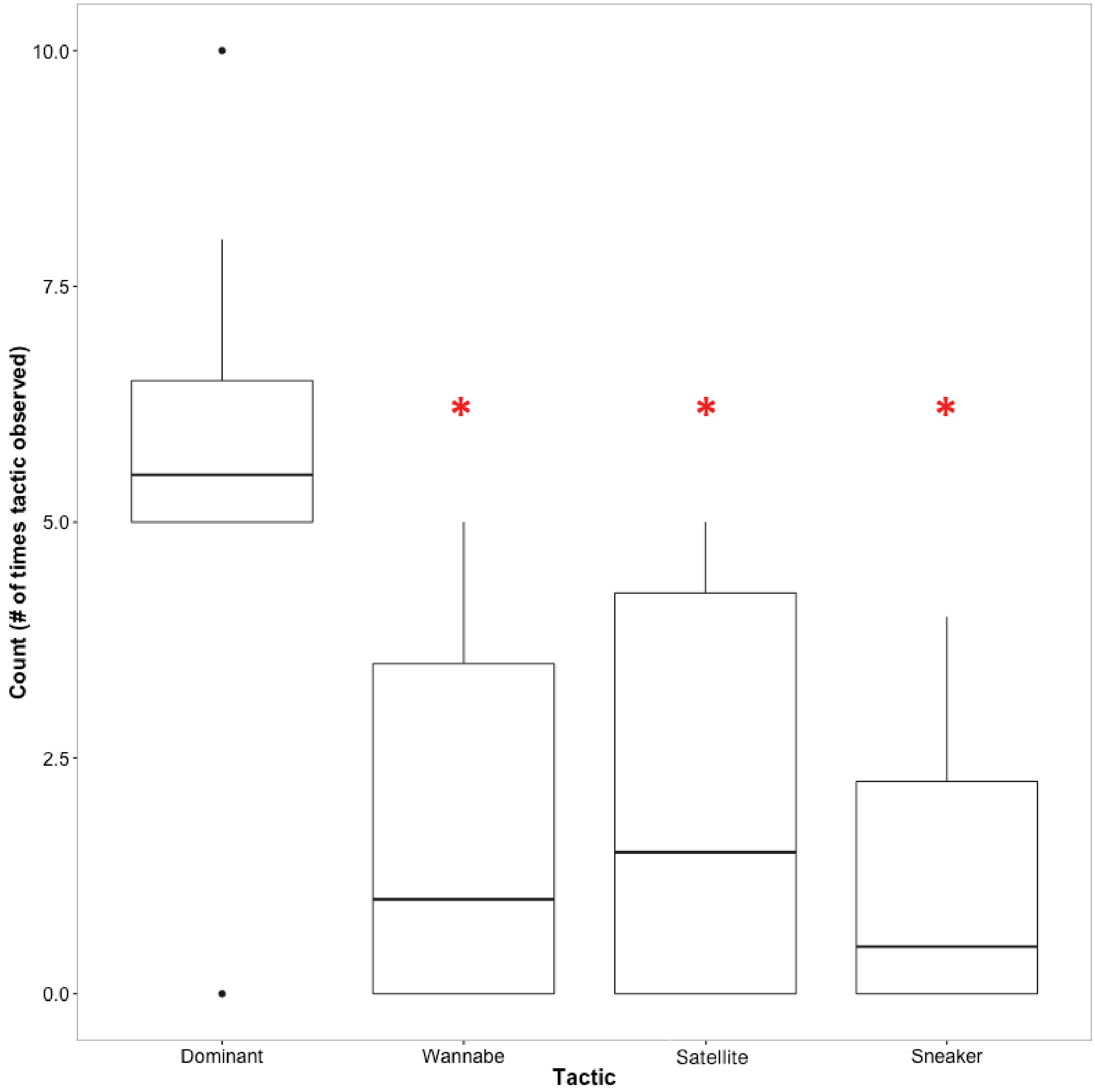


Figure 5: Male mating tactics represented as the number of occurrences (counts) summed up from presence/absence data for each day of every trial. Closed black circles represent outliers while the red asterisks are above male mating tactics with p-values < 0.05.

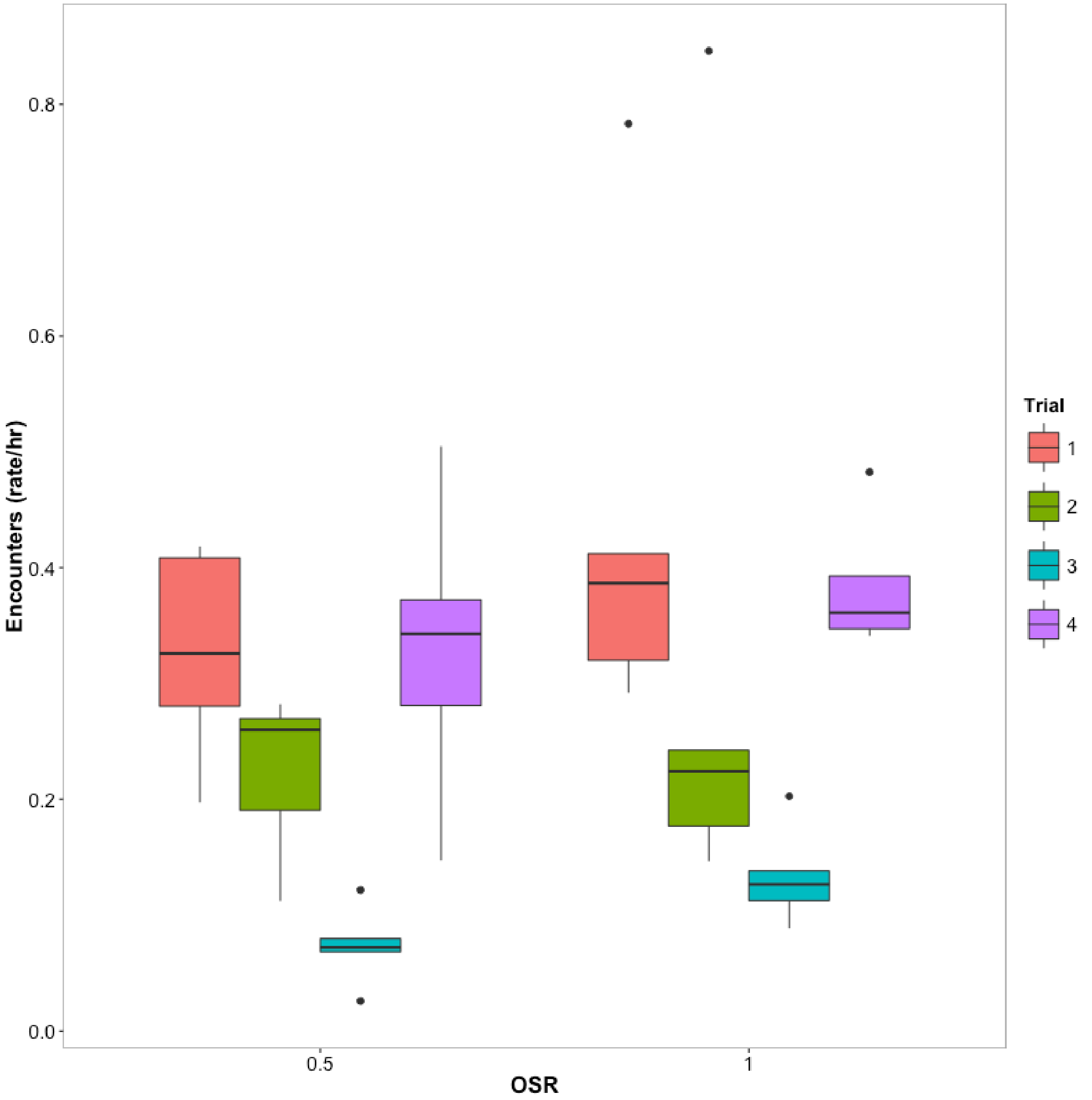


Figure 6: Encounter rates measured as the number of encounters between two individuals within a 2 m radius which did and did not result in an agonistic engagement. Rate is calculated as a mean per hour. Closed black circles represent outliers.

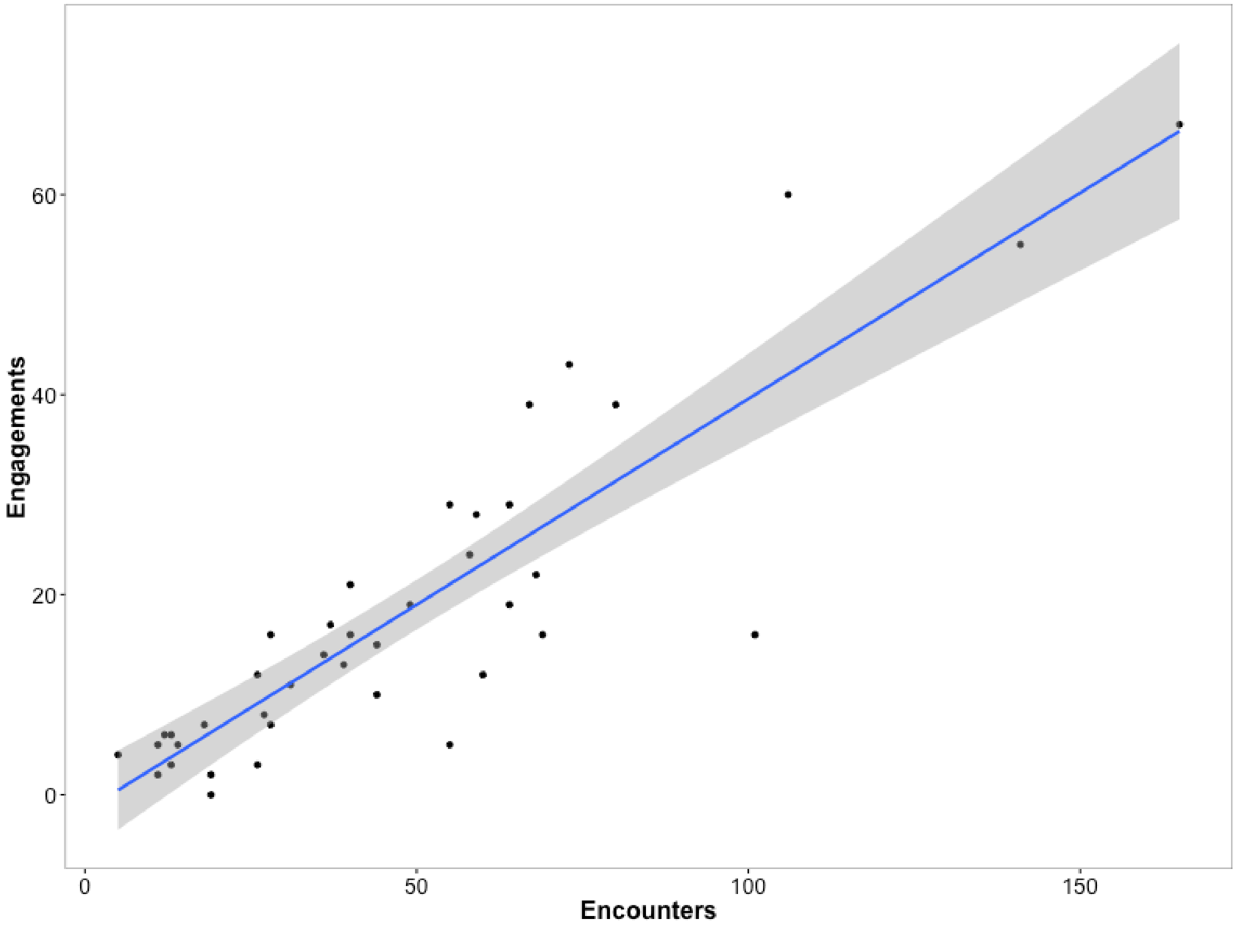


Figure 7: Relationship between number of engagements in relation to encounter frequency. The black dots represent all data collected from the field for both number of engagements and number of encounters during all trials (N = 4). The blue line represents the model predictions and the grey area represents the 95% confidence interval.

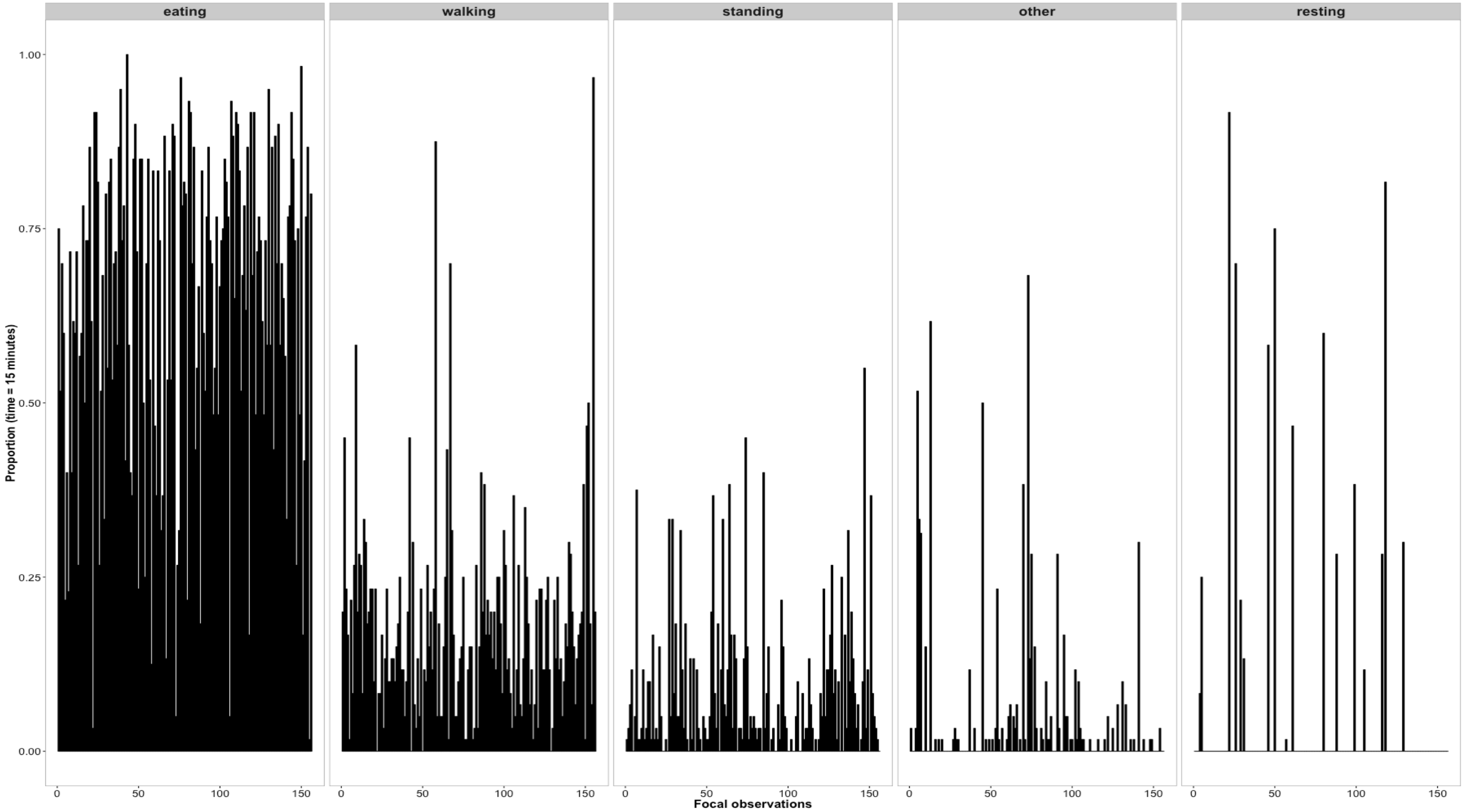


Figure 8: Male focal observations quantifying and comparing proportions of a witnessed behaviour over time (t = 15 minutes). Each bar represents one focal observation (N = 150) in any given treatment on one individual. Behaviours organized from most prominent to least (left – right).

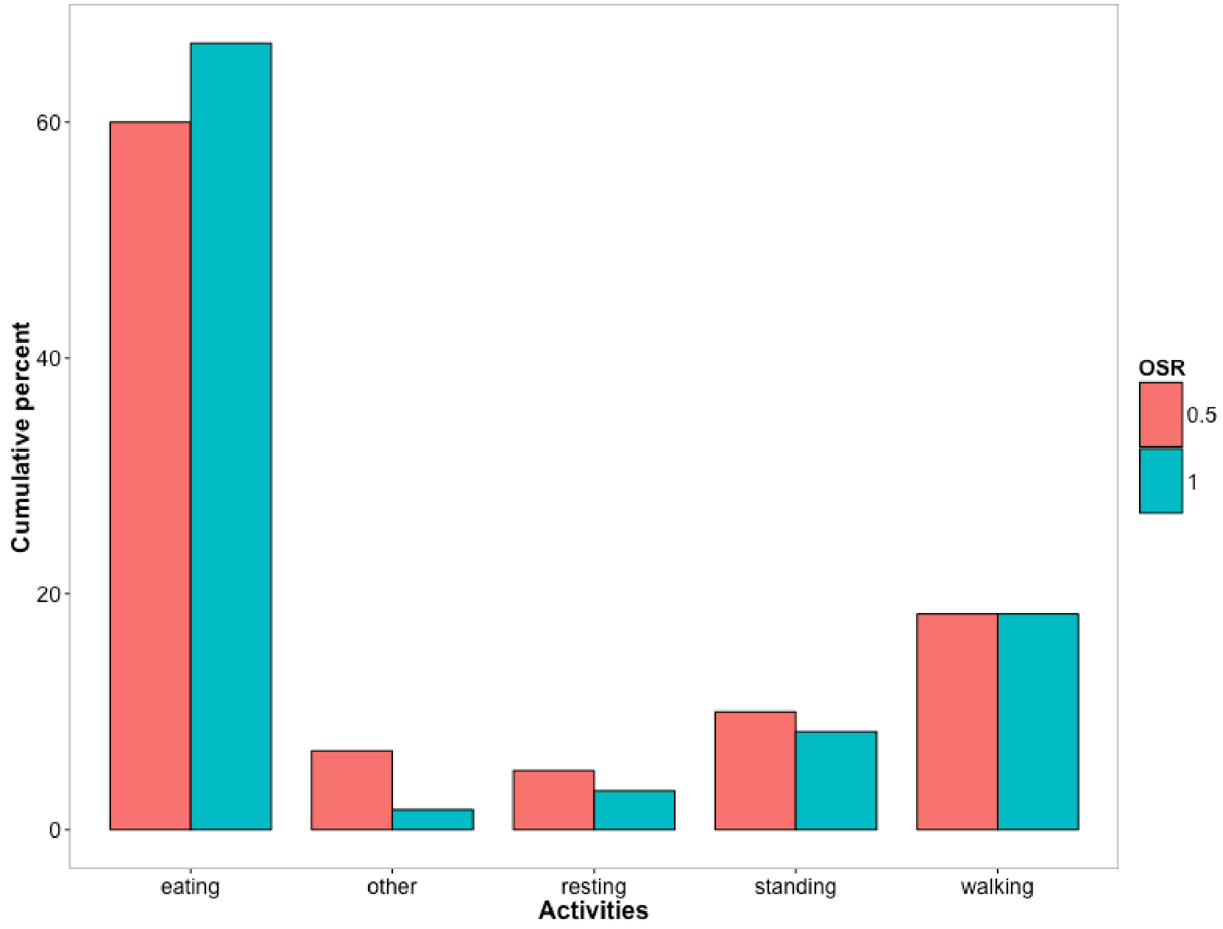


Figure 9: Mean male activities tallied over the length of the experiment (N = 4). Bars represent mean values for all individuals in a treatment over a 4 week observation period.

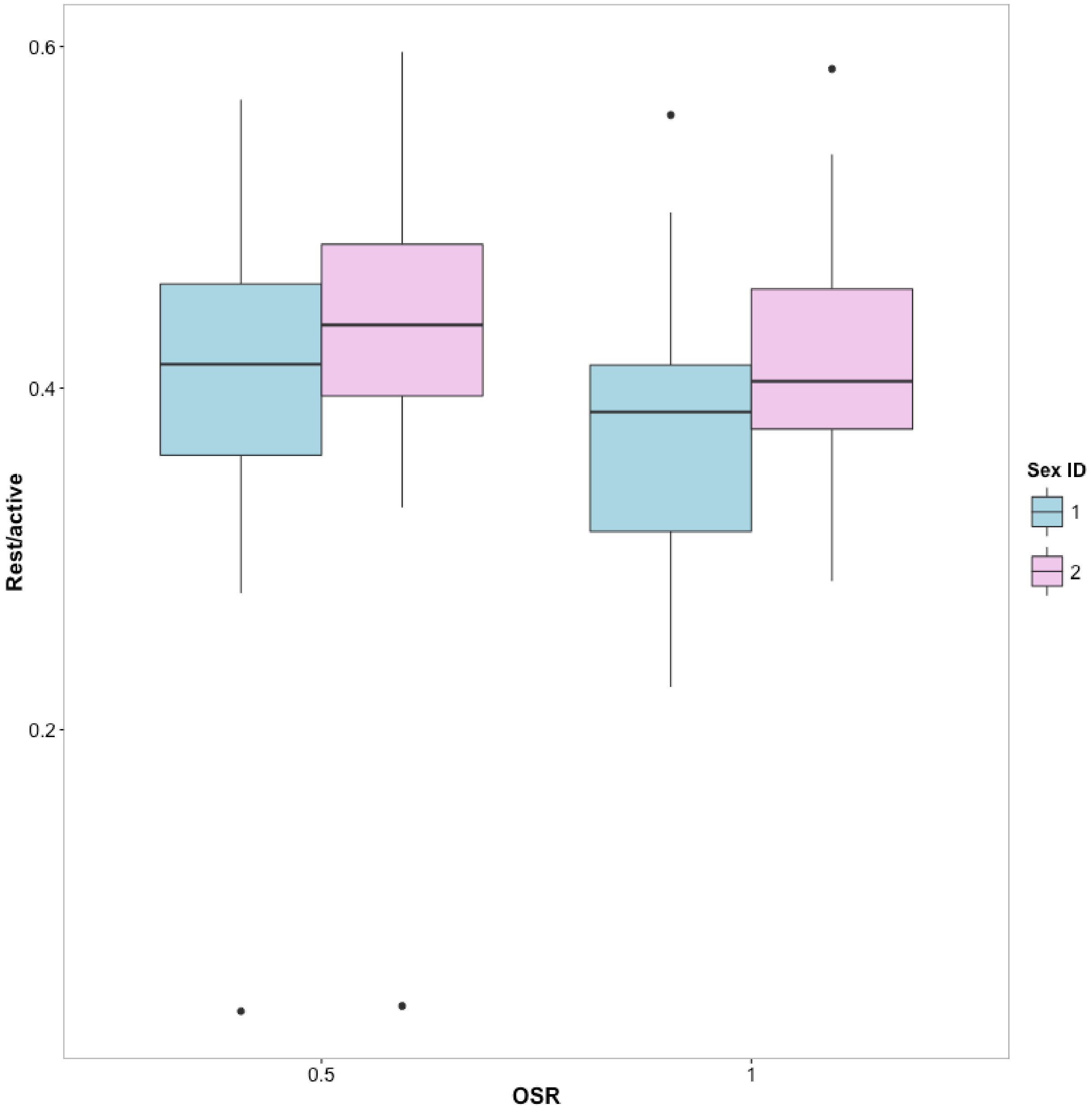
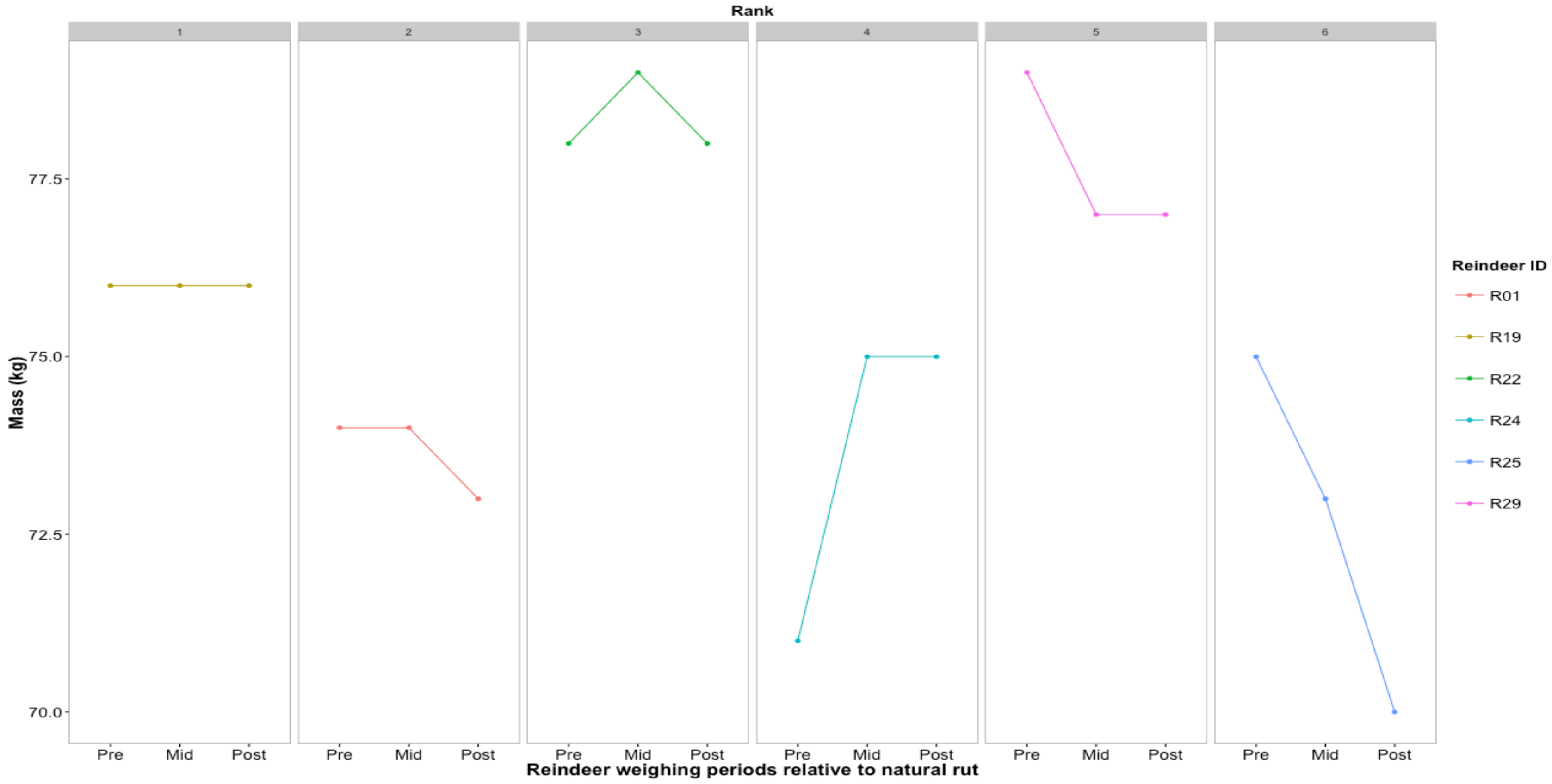


Figure 10: Rest/active periods of both male and female reindeer. Rest/active times were computed for every individual and pooled daily by sex and OSR level over the length of the experiment (N = 4).

APPENDIX



Appendix A: Male reindeer rate of mass gain/loss based on final ranks established through MatMan 6 x 6 matrix. Pre-rut weight (September 22nd) was taken before the study began. Mid-rut weight (October 4th) was taken after trial 2, Post-rut weight (October 19th) was taken a few days after the end of trial 4. All individuals had the opportunity to interact with each other throughout the experiment with the exception of R25 (rank 6) and R29 (rank 5) by random chance alone. Their final ranks were determined solely on the number of agonistic wins and losses throughout the experiment (see Appendix B).

Appendix B: These matrices represent male-male agonistic interactions between three males every trial in every OSR. Due to the non-significant p-values from the MatMan table, we felt it necessary to include the matrices to show how the social hierarchy reflected is highly linear and this has biological significance. When read from left to right, choose a reindeer ID and the value to the right indicate the number of won agonistic interactions to the male reindeer ID in the same column as the value. When read from top to bottom, choose a reindeer ID and the value indicates the number of lost agonistic interactions to the male reindeer ID in that row.

Trial 1 OSR 0.5	R19	R24	R29
R19	*	4	0
R24	24	*	4
R29	17	19	*

Trial 1 OSR 1	R01	R22	R25
R01	*	3	2
R22	19	*	4
R25	70	45	*

Trial 2 OSR 0.5	R19	R24	R25
R19	*	0	0
R24	10	*	1
R25	24	43	*

Trial 2 OSR 1	R01	R22	R29
R01	*	3	1
R22	28	*	1
R29	68	44	*

Trial 3 OSR 0.5	R22	R24	R29
R22	*	0	0
R24	9	*	0
R29	48	41	*

Trial 3 OSR 1	R01	R19	R25
R01	*	3	0
R19	1	*	0
R25	57	27	*

Trial 4 OSR 0.5	R22	R24	R25
R22	*	0	0
R24	45	*	2
R25	57	106	*

Trial 4 OSR 1	R01	R19	R29
R01	*	9	0
R19	2	*	0
R29	26	21	*