

1 **Influence of operational sex ratio and male age on mating competition**  
2 **intensity in reindeer (*Rangifer tarandus*)**

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22 **Influence of operational sex ratio and male age on mating competition intensity in**  
23 **reindeer (*Rangifer tarandus*)**

24         The operational sex ratio (OSR), the ratio of sexually active males to sexually  
25 receptive females, is one of the main measures used to predict the intensity and  
26 direction of mating competition, influencing the opportunity for sexual selection. Here,  
27 we conducted the first experimental study to investigate how OSR and male age impacts  
28 the intensity of mating competition in reindeer (*Rangifer tarandus*), under semi-natural  
29 conditions during the rut. We manipulated OSR on two levels in two enclosures, a  
30 female biased treatment (3♂:6♀ = OSR 0.5) and a sex balanced treatment (3♂:3♀ =  
31 OSR 1), over two years with males from two age groups, and with females of various  
32 ages. We found some support for prevailing OSR theory, notably with female  
33 intrasexual competition occurring at lower frequencies in OSR 1 than OSR 0.5, and  
34 male intrasexual competition occurring at higher frequencies in the older male age  
35 group. Courtship behaviour was found to occur at higher frequencies in OSR 1 than  
36 OSR 0.5, however, there was no effect of male age. To successfully pass on genes to  
37 the next generation, one needs access to mates and winning a competitive bout is not  
38 always indicative of successfully accomplishing gene flow. Studies on OSR have the  
39 potential to help us understand the drivers behind sexual competition and how best to  
40 predict breeding outcomes during a rut.

41         Keywords: sexual selection, animal behaviour, mating systems,  
42         operational sex ratio, *Rangifer tarandus*, intrasexual competition

43

## INTRODUCTION

44

45 Over the last five decades, there has been a significant body of research  
46 investigating the ecological factors that promote differences in the intensity of sexual  
47 selection, both within and among species. While the intensity of sexual selection largely  
48 depends on the level of competition for mates, the degree of competition depends on  
49 two factors: the difference in parental investment of the two sexes and the operational  
50 sex ratio (Krebs & Davies 1987). Operational sex ratio (OSR) is considered one of the  
51 main predictors for the intensity and direction of mating competition (Kvarnemo &  
52 Ahnesjo 1996), where it represents the ratio of sexually active males to sexually  
53 receptive females, in a given breeding group, at a given time. When the OSR is biased  
54 towards one sex, it is expected that there will be more intense competition among  
55 members of the non-limiting sex for access to the limiting sex (Clutton-Brock & Parker  
56 1992). The intensity and direction of biases in OSR can be influenced by the potential  
57 reproductive rates (PRR) of the sexes (Clutton-Brock & Parker 1992), the spatial and  
58 temporal distribution of the sexes (Krupa & Sih 1993), the adult sex ratio (ASR) of the  
59 population, differences between the sexes in age at maturity (Pitnick 1993),  
60 reproductive longevity, migration schedules, and mortality rates (Iwasa & Odendaal  
61 1984).

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

70 Overall, across various taxa, most studies support the OSR based predictions for  
71 the occurrence of intrasexual competition among males (Emlen & Oring 1977; Janicke  
72 & Morrow 2018; Weir et al. 2011); however, the literature is less consistent when  
73 investigating male courtship behaviour. Traditional OSR theory predicts that male  
74 courtship rates will increase as the OSR becomes increasingly more male biased (Emlen  
75 & Oring 1977; de Jong et al. 2012), however, many studies show the exact opposite  
76 trend (Chuard et al. 2016; Verrell & Krenz 1998; Weir et al. 2011). It has been

77 suggested that this trend could simply be due to females being limited in supply within  
78 male biased OSR treatments; therefore, if male competition increases with OSR, there  
79 will be less opportunity to engage in courtship displays (de Jong et al. 2012; Jirotkul  
80 1999).

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

90 Among wild populations of mammals, great variation exists in the abundance of  
91 male and females within a group due to sex specific patterns in mortality rates (see:  
92 Berger & Gompper 1999). Ungulate species exemplify this range of variation, such as  
93 with wild goat (*Capra aegagrus*), where the ASR can be as high as 1.42 males per  
94 female, or as low as 0.22 males per female, as is the case with the African buffalo  
95 (*Syncerus caffer*; Husband & Davis 1984; Prins & Iason 1989). Within cervidae,  
96 reindeer (*Rangifer tarandus*) represent an ideal opportunity for studying mate  
97 competition in relation to variation in sex ratios. Males of this species exhibit harem  
98 defense polygyny during a well-defined rutting period, where the gregariousness of  
99 females allows males to directly monopolize them (Espmark 1964; Geist 1999;  
100 Melnycky et al. 2013; Skogland 1989). The reproductive success of male reindeer has  
101 been shown to be highly skewed as well, with the older more dominant individuals  
102 siring the most calves (Røed et al. 2002). Sex ratio has also been found to be an  
103 important factor for influencing variance in male reindeer reproductive success. As the  
104 ratio becomes more balanced, older dominant males switch from guarding large groups  
105 of females to restricting access to individual females that are in oestrus (Røed et al.  
106 2002). Due to a lack of paternal care in this species, males can devote a considerable  
107 amount of energy towards reproduction, where they perform intensive fighting and  
108 courting behaviour (Espmark 1964; Skogland 1989). These high energy competitive  
109 interactions between individuals result in considerable somatic costs during the rut

110 (Holand et al. 2012; Mysterud et al. 2003). Finally, since reindeer are a semi-  
111 domesticated species and are maintained under semi-natural conditions, they provide an  
112 excellent opportunity to experimentally investigate the influence of OSR on the  
113 reproductive behaviour of a mammalian species.

114 The aim of the present study was to use an experimental approach to investigate  
115 how the rutting behaviour of 1.5 and 2.5-year-old male reindeer is influenced by either a  
116 balanced OSR ( $3\text{♂}:3\text{♀} = \text{OSR } 1$ ) or a female-biased OSR ( $3\text{♂}:6\text{♀} = \text{OSR } 0.5$ ), in an  
117 effort to expand the generalizability of present mating systems theory. Due to the rarity  
118 of studies in OSR literature investigating both male and female reproductive behaviour  
119 simultaneously, we also incorporated female rutting behaviour in our design. Based on  
120 prevailing OSR theory we can make several predictions. (1) Higher frequency of male-  
121 male competition is predicted for the OSR 1 treatment in comparison to OSR 0.5,  
122 whereas the opposite is predicted for the frequency of female intrasexual competition.  
123 (2) Similar to many other ungulate species, reindeer are polygynous and exhibit  
124 conventional sex roles; therefore, it is expected that males will engage in higher levels  
125 of intrasexual competition than females regardless of the OSR treatment. And (3) the  
126 frequency of male courtship behaviour is predicted to be higher in OSR 1 due to the  
127 utilization of alternative mating tactics. Similar to various other taxa, male reindeer  
128 exhibit age-dependent differences in reproductive effort and mating tactic utilization  
129 (Tennenhouse et al. 2012), therefore the following predictions can be made on age  
130 specific responses: (i) older males are expected to engage in higher intrasexual agonistic  
131 encounters compared to younger males in OSR 1 and (ii) it is expected that courtship  
132 rate will be higher among the 2.5-year-old males than 1.5-year-old males.

## 133 MATERIALS AND METHODS

### 134 *Ethics Statement*

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

139 *Study Location and Research Herd*

140 Behavioural sampling occurred over the course of two field seasons, at the  
141 Kutuharju Experimental Reindeer Research Station maintained by the Reindeer  
142 Herder's Association, near Kaamanen in Northern Finland (69°N, 27°E). Sampling for  
143 the first field season utilized 2.5-year-old male reindeer and went from September 29<sup>th</sup> –  
144 October 15<sup>th</sup>, 2016. The second field season utilized 1.5-year-old male reindeer, and  
145 sampling occurred from October 1<sup>st</sup>, 2017 – October 17<sup>th</sup>, 2017. The research station's  
146 total area is 45 km<sup>2</sup>. Two fenced enclosures were utilized for each field season, both  
147 with an area of 0.5 km<sup>2</sup>, and shared 0.4 km of fencing. These areas are largely  
148 characterized by birch (*Betula spp.*) and Scots pine (*Pinus sylvestris*) forests, along with  
149 the presence of many bogs and lakes (L'Italien et al. 2012).

150 *Experimental Design*

151 The OSR was manipulated on two levels, a female biased OSR of 0.5 (3♂:6♀)  
152 and a balanced OSR of 1 (3♂:3♀), to investigate its impact on inter and intra-sexual  
153 competition. Female ungulates typically exhibit a short and highly synchronous oestrus  
154 (de Vos et al. 1967); therefore, it is expected that the number of females in oestrus will  
155 follow an inverse U – shaped pattern. This results in many females being in oestrus  
156 during peak rut, and very few during early and late rut (Hirotsani 1989). In a managed  
157 population, where the number of mature males remains constant, OSR is predicted to  
158 follow an inverse U – shaped pattern, with a maximum during peak rut, resulting in  
159 fewer individuals ready to reproduce during early and late rut. Considering this pattern,  
160 a male biased OSR is likely to put males at risk of injury and was thus omitted as a  
161 possibility in this study to avoid animals being harmed.

162 A total of 6 male reindeer (either 1.5 or 2.5-years-old) and 27 female reindeer  
163 (mixed age) were included in each field season. To ensure that any effect of treatment  
164 on male behaviour was due to OSR alone, both male age and density were kept  
165 constant, resulting in only 2.5-year-old males being utilized in 2016 and only 1.5-year-  
166 old males being utilized in 2017. Male reindeer in each study year were fitted with very  
167 high frequency (VHF) collars to allow tracking of breeding groups in the enclosures  
168 using radio telemetry. Both field seasons consisted of three trials, each with a duration  
169 of 5 days, and were separated by an acclimation day. At the beginning of each trial, the  
170 same six males were haphazardly ordered into one of two enclosures by local reindeer

171 herders, whereas 9 new females were separated at random into either enclosure for each  
172 trial representing either an OSR of 0.5 or 1. Additionally, between each trial, the OSR  
173 assignment for the enclosures was rotated randomly.

174 Due to the relatively large-scale nature of this study, with many recording  
175 techniques and the use of two enclosures simultaneously, data was collected by two  
176 observers. Prior to the start of each field season, both observers agreed on descriptions  
177 of the behaviours to be examined and a shared ethogram was constructed (Table 1).  
178 During this pre-field season time frame, data was collected simultaneously by both  
179 observers to calculate the index of concordance for behavioural sampling, ensuring both  
180 observers were accurately recording the same behaviours (Martin & Bateson 2007). The  
181 index of concordance was 88% for behavioural sampling and 98.3% for focal sampling  
182 in the 2016 field season. For the 2017 field season, the index of concordance was 93%  
183 for behavioural sampling and 99.5% for focal sampling.

#### 184 *Oestrus Synchronization*

185 To ensure the successful synchronization of female receptivity during the rut, a  
186 two-injection protocol of estrumate® (cloprestenol sodium), a synthetic analogue of  
187 prostaglandin that promotes oestrus in cattle, was utilized (Hardin et al. 1980; Johnson  
188 1978; Odde 1990). Due to its success with cattle species and its wide safety margin for  
189 both the treatment receiving females and produced progeny, estrumate was deemed a  
190 safe treatment for our study species (MSD Animal Health 2013). Females were injected  
191 intramuscularly with 1 mL of estrumate (0.25 mg cloprestenol sodium) by a registered  
192 veterinarian with experience administering the hormone. Once the first injection was  
193 completed, a 10-day lag period commenced prior to receiving a second injection. After  
194 the second injection they were herded into their experimental enclosures. In normal  
195 cycling cattle, oestrus is expected to occur 2-5 days following the second injection. It is  
196 also important to note that females were kept in a separate enclosure away from males  
197 to ensure copulation did not occur before any trial commenced.

#### 198 *Behavioural Observations*

199 Agonistic and courtship data were collected using behavioural sampling,  
200 whereby groups of both sexes were continuously observed for a period of 15 minutes,  
201 with a total of 45 minutes of sampling per hour. For behavioural sampling to occur,

202 half the group or more needed to be visible to the observer. A group is defined to be a  
203 cluster of individuals within 100m of each other, comprising of two or more individuals,  
204 regardless of their sex and are separated by 100m from another group (Tennenhouse et  
205 al. 2011). The behaviours of interest for this sampling were: chase, spar, fight, displace,  
206 head threat, attempted copulation, copulation, mate guarding, bush thrashing, scent  
207 marking, sneaking, follow, court, herd, grunt and flehmen (Espmark 1964; Tennenhouse  
208 et al. 2012). Additionally, the identity of the individuals involved were identified and  
209 recorded in the field using binoculars, along with the interaction type, classified as:  
210 male-male (M-M), female-female (F-F), or male-female (M-F).

### 211 *Statistical Analysis*

212 Generalized linear mixed models (GLMMs) were used to analyze the intensity  
213 of intra- and inter-sexual interactions, and male focal behaviours by using the  
214 ‘lme4’ package (Bates et al. 2015). Co-linearity between variables was assessed by  
215 calculating the variance inflation factor (VIF), where if  $VIF > 2.5$ , the predictors  
216 involved were removed from the model. Both OSR and male age were found to have  
217 VIF values of 1.0, therefore they were utilized as predictors. Applying a backwards  
218 stepwise approach to model selection fit, we first assessed if any interaction terms were  
219 significant. If the interaction was non-significant, the term was dropped from the model.  
220 All models were fitted with a Poisson distribution and a log link function. If  
221 overdispersion was detected, the GLMMs were fitted with a negative binomial  
222 distribution. Regardless of the behaviour of interest, reindeer ID was assigned as a  
223 random factor in every model to control for non-independence of observations due to  
224 the same six males being observed across the three trials per year (Thiele & Markussen  
225 2012).

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



233 the response variable. These GLMMs assessed whether male courtship varied between  
234 OSR treatments, male age, or if there was a significant interaction between the two.

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

## 237 RESULTS

### 238 *Agonistic Interactions*

239 Female intrasexual agonistic interactions were found to occur at significantly  
240 lower frequencies in OSR 1 (parameter estimate = -0.5694, 95% CI = -0.97-1.72, -  
241 0.14182;  $p < 0.05 = 0.015$ ; see Fig. 1a). The frequency of male intrasexual agonistic  
242 interactions were not found to vary significantly with OSR (parameter estimate = 0.12,  
243 95% CI = -0.22, 0.47;  $p = 0.49$ ); however, there was a significant trend for male-male  
244 agonistics to be higher for 2.5-year-old males than 1.5-year-old males (parameter  
245 estimate = -0.50, 95% CI = -0.95, -0.054;  $p < 0.05$ ; Fig. 1b). With respect to male-female  
246 agonistic interactions a marginally significant difference was found for OSR (parameter  
247 estimate = -0.43, 95% CI = -0.86, 0.0092;  $p = 0.055$ ; Fig. 1c), suggesting that male-  
248 female agonistic interactions occurred at higher frequencies in OSR 0.5. Lastly, the  
249 interaction term for OSR and sex for male and female intrasexual agonistic interactions  
250 was found to be significant (parameter estimate = -0.61, 95% CI = -1.14, -0.091;  $p <$   
251  $0.05$ ; Fig. 1d), suggesting that males and females engaged in differing frequencies of  
252 intrasexual agonistic interactions depending on OSR.

### 253 *Male Courtship*

254 The frequency of occurrence of male courtship behaviours was not found to vary  
255 significantly with male age (parameter estimate = -0.49, 95% CI = -1.22, 0.25;  $p = 0.19$ ).  
256 In contrast, a significant difference was found for the effect of OSR (parameter estimate  
257 = 0.56, 95% CI = 0.016, 1.1;  $p < 0.05$ ), with courting behaviours occurring more  
258 frequently in OSR 1 (Fig. 2).

## 259 DISCUSSION

260 Operational sex ratio is thought to be one of the main predictors of the intensity  
261 and direction of mating competition (Kvarnemo & Ahnesjo 1996). In this study, we

262 exposed 1.5 and 2.5-year-old male reindeer to two different OSR treatments, to  
263 investigate whether OSR and male age played an important role in the intensity of  
264 mating competition.

265 We found support for a higher frequency of female-female agonistic encounters  
266 in OSR 0.5 vs OSR 1. Among female mammals, there are high energetic costs  
267 associated with maternal care, such as with gestation and lactation, resulting in direct  
268 resource competition among females (Rosvall 2011). However, it has been shown that  
269 females, like males, do compete for access to mates, through activities such as threat  
270 displays (ex: Vervet monkeys, *Chlorocebus pygerythrus*; Horrocks & Hunte 1983),  
271 punishment (ex: Cleaner wrasse, *Labroides dimidiatus*; Raihani et al. 2010), harassment  
272 (ex: Gelada baboons, *Theropithecus gelada*; Dunbar & Dunbar 1977; ex: Moose, *Alces*  
273 *alces*; Miquelle 1991), reproductive suppression (ex: Damaraland mole rat, *Fukomys*  
274 *damarensis*; Young et al. 2010), and less commonly, fights (ex: Meerkats, *Suricata*  
275 *suricata*; Clutton-Brock & Huchard 2013; Sharp & Clutton-Brock 2011). In some  
276 ungulates that exhibit harem defense during a well-defined mating season, it is common  
277 for there to be synchrony of sexual receptivity among females, resulting in competition  
278 among females for the attention of males (Bro-Jorgensen 2002, 2011). A strong case for  
279 evidence that mate limitation could drive female competition, as predicted by OSR  
280 theory, was observed in the saiga antelope (*Saiga tatarica*), after poaching created a  
281 heavily biased sex ratio towards females, resulting in dominant females aggressively  
282 excluding subdominant females from mating (Milner-Gulland et al. 2003).

283 It has been suggested that one of the main causes for female-female mate  
284 competition among ungulate species arises from sperm limitation, occurring from males  
285 engaging in high rates of mating during peaks of rutting activity. Sperm limitation is  
286 promoted by factors such as female promiscuity, synchronized breeding and strong  
287 female mate preferences, resulting in fewer males being considered as eligible mates  
288 (Ahnesjo et al. 2001; Bro-Jorgensen 2011). Female reindeer exhibit a short and highly  
289 synchronous oestrus, with most females entering oestrus during peak rut.

290 Approximately 90% of females breed in a 10-21-day period, with calving occurring the  
291 following spring (Bergerud 1975; Dauphiné & McClure 1974; Ropstad et al. 1996;  
292 Rowell & Shipka 2009). Males in this study herd typically copulate with most females  
293 during peak rut (Weladji et al. 2017). We found that 2.5-year-old males engaged on  
294 average in more courting behaviours on day 2 of each trial, coinciding with when

295 oestrus was expected to be induced for most of our females. It is plausible that the  
296 higher female-female agonistic encounters we observed in OSR 0.5 supports the idea of  
297 females competing for the fittest mate. Specifically, in OSR 0.5 where males are the  
298 limiting sex, aggressive interference among females might be a strategy for the winner  
299 to successfully acquire the fittest mate's sperm by avoiding sperm depletion if the fittest  
300 mate first breed other females. Thus, such agonistic encounters between females could  
301 be functioning as a way to gain the attention of desired mates, thereby increasing the  
302 probability of mating for aggressive females (Clutton-Brock 2009; Baniel et al. 2018).  
303 This concept has been proposed with the topi antelope (*Damaliscus lunatus jimela*),  
304 where females in oestrous who engaged in higher frequencies of agonistic interactions,  
305 increased their chances of mating with the favoured mate (Bro-Jorgensen 2007). This  
306 could also lead to a situation where male choosiness comes into play when male mating  
307 rates are being constrained by female efforts to monopolize mating opportunities with  
308 preferred males (Bebie & McElligott 2006; Bro-Jorgensen 2007, 2011).

309         While this result increases our understanding of female-female interactions, it is  
310 important to acknowledge, that we did not control for female density or absolute  
311 density, therefore it is difficult to conclude that this effect on female-female agonistic  
312 interactions was entirely due to OSR and not a density related effect or an interaction  
313 between the two. Kokko and Rankin (2006) proposed that competition for mating  
314 opportunities would be correlated with density, where dominant individuals will have  
315 more opportunity to monopolize mates at higher population densities, thereby leading to  
316 an increase in the potential for sexual selection with increased density. Both population  
317 density and OSR are not independent of one another and together likely influence  
318 sexual selection by affecting the encounter rate of mates (Clutton-Brock & Parker  
319 1992). Within the literature, there is contradictory evidence on the influence of density  
320 on competition intensity for mates. Some studies support the predicted increase in  
321 intrasexual competition with population density (Jirotkul 1999; Smith & Sargent 2007;  
322 Lauer et al. 1996), while others appear to oppose or show no clear support of these  
323 predictions (McLain 1992; Head et al. 2008; de Jong et al. 2009).

324         Though we did not find support for the prediction that agonistic interactions  
325 between males would occur at higher frequencies in OSR 1, male age did significantly  
326 impact the rate of agonistic interactions. Agonistic interactions were witnessed at higher  
327 rates in 2.5-year-old males than 1.5-year-old males regardless of OSR. It is plausible

328 that our lack of support for varying OSRs influencing intrasexual competition among  
329 male reindeer could be adding to evidence that suggests the predictive effects of OSR  
330 on mate competition varies between species and may not be as generalizable as  
331 previously thought (e.g.: Balshine-Earn 1996; de Jong et al. 2009; Wacker et al. 2013).  
332 The significant difference in male-male agonistic interactions in 2.5-year-old males  
333 compared to 1.5-year-old males suggest that though both age groups are not fully  
334 considered adults even though they are reproductively active, the additional year of  
335 experience the 2.5-year-old males have during a rut, is significant enough to influence  
336 the intensity of competition for mates more so than the younger males (Myserud et al.  
337 2003; Myserud et al. 2004).

338         Within the literature there is a discrepancy in courtship results when comparing  
339 between laboratory and field studies (see: de Jong et al. 2009). Typically, field studies  
340 support the idea that OSR regulates mating competition, whereas laboratory studies  
341 commonly report results that are contradictory to traditional OSR theory. A meta-  
342 analysis by Weir et al. (2011) revealed that competitive behaviours do not always  
343 increase linearly with an increasing OSR bias towards the competitor's own sex. This  
344 result highlights that the nature of the relationship is context dependent, and the type of  
345 mating behaviour being investigated can be an example. Denoël et al. (2005) did not  
346 report significant differences in courting behaviour and agonistic interactions of alpine  
347 newt (*Triturus alpestris*) males between male biased OSRs or balanced OSRs. Contrary  
348 to the findings of laboratory studies and in line with traditional OSR theory in the field,  
349 our research demonstrated that the rate of male courtship was present at higher  
350 frequencies in OSR 1 vs OSR 0.5, independent of male age. In the sex balanced OSR,  
351 OSR 1, males have fewer possibilities to control a harem without other males  
352 challenging them for the same females given the limited availability of mates.  
353 Therefore, it may be possible that in OSR 1 where it is more costly to engage in male-  
354 male agonistic interactions, the mating strategy is to increase the frequency of courtship  
355 displays thereby also providing an opportunity for females to choose their mate. In OSR  
356 0.5 where there are more females to males, it may be too risky to focus on the more  
357 passive courtship displays as opposed to being more aggressive with agonistic  
358 interactions and winning the female over.

359         Moreover, it was recently suggested that due to the dynamic nature of OSR  
360 during the reindeer rutting season, the intensity of mating competition may not be a

361 main driver for male mating behaviour. This was supported by the observation that male  
362 mating behaviour followed a pattern of adjustment in accordance with the time of the  
363 rut and social environment (Weladji et al. 2017). Further suggesting that other factors  
364 should be considered along with OSR as researchers attempt to expand classic  
365 predictions across various taxa. In fact, a myriad of other factors impact competition for  
366 mates, such as mortality (Okuda 1999), the cost of reproduction (Kokko & Monaghan  
367 2001), mate quality (Johnstone et al. 1996), and density (Kokko & Rankin 2006).

368 In summary, we found support for predictions based on OSR theory with respect  
369 to female-female agonistic encounters occurring at lower frequencies in OSR 1; and that  
370 under the same OSR, male-male agonistic encounters would occur at greater  
371 frequencies compared to OSR 0.5. We did also find support for our prediction of  
372 conventional sex roles based on OSR theory, where the frequency of occurrence of  
373 intrasexual agonistic encounters varied based on the reindeer being male or female and  
374 the OSR treatment involved, with males engaging in higher frequencies overall. We did  
375 not find support for our prediction that male courtship would have lower frequencies of  
376 occurrence in OSR 1 due to a rise in male-male agonistic encounters.

377 Furthermore, the evidence we presented here, highlighting age contrasts in  
378 behavioural maturity of reindeer males, may serve as a cautionary piece of information  
379 for herd management. While, male reindeer are technically sexually mature by 17-18  
380 months old, their lack of previous rutting experience leaves them at a disadvantage with  
381 respect to acquiring mates (McEwan 1963). Maintaining young male age class structure  
382 and female biased sex ratios, may potentially result in younger males not properly  
383 developing strong courting strategies due to the lack of older and experienced  
384 individuals to learn from, which can lead to delays in calving, lower birth synchrony,  
385 delay the development of body mass, and shifts in offspring sex ratio (Milner et al.  
386 2007).

387 Although we did observe some support of prevailing OSR theory, our results on  
388 male-male agonistic and male courtship add to a growing body of evidence in the  
389 literature showcasing that the predicted positive relationship between mating  
390 competition and OSR may be an oversimplification (Klug et al. 2010), such that the  
391 value of OSR as a predictor of mating competition likely varies between species and  
392 ecological conditions. Our emerging trends based on male age cohort comparison,  
393 further highlight the importance of considering other factors that impact competition for

394 mates, such as prime reproductive age. This is especially true for future research aiming  
395 to expand the generalizability of OSR theory to a wider range of taxa and ecological  
396 conditions.

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#### 404 DISCLOSURE STATEMENT

405 The authors declare that they have no competing interests.

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#### 412 REFERENCES

- 413 Ahnesjö I, Kvarnemo C, Merilaita S. 2001. Using potential reproductive rates to predict  
414 mating competition among individuals qualified to mate. *Behav Ecol.* 12(4):397-  
415 401.
- 416 Balshine-Earn S. 1996. Reproductive rates, operational sex ratios and mate choice in St.  
417 Peter's fish. *Behav Ecol Sociobiol.* 39(2):107-116.

418 Baniel A, Cowlshaw G, Huchard E. 2018. Context dependence of female reproductive  
419 competition in wild chacma baboons. *Anim Behav.* 139:37-49. doi:  
420 10.1016/j.anbehav.2018.03.001

421 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models  
422 Using lme4. *J Stat Soft.* 67(1):1-48.

423 Bebie N, McElligott AG. 2006. Female aggression in red deer: Does it indicate  
424 competition for mates? *Mam Biol.* 71(6):347-355. doi:  
425 10.1016/j.mambio.2006.02.008

426 Berger J, Gompper ME. 1999. Sex Ratios in Extant Ungulates: Products of  
427 Contemporary Predation or Past Life Histories? *J Mam.* 80(4):1084-1113.

428 Bergerud AT. 1975. The reproductive season of Newfoundland caribou. *Can J Zool.*  
429 33:1213-1221.

430 Bro-Jorgensen J. 2002. Overt female mate competition and preference for central males  
431 in a lekking antelope. *Proc Nat Acad Sc USA.* 99(14):9290-9293. doi:  
432 10.1073/pnas.142125899

433 Bro-Jorgensen J. 2007. Reversed sexual conflict in a promiscuous antelope. *Curr Biol.*  
434 17(24):2157-2161.

435 Bro-Jorgensen J. 2011. Intra- and intersexual conflicts and cooperation in the evolution  
436 of mating strategies: lessons learnt from ungulates. *Evol Biol.* 38(1):28-41.

437 Chuard PJC, Brown GE, Grant JWA. 2016. The effects of adult sex ratio on mating  
438 competition in male and female guppies (*Poecilia reticulata*) in two wild  
439 populations. *Behav Proc.* 129:1-10.

440 Clutton-Brock TH. 2009. Sexual selection in females. *Anim Behav.* 77(1):3-11. doi:  
441 DOI: 10.1016/j.anbehav.2008.08.026

442 Clutton-Brock TH, Huchard E. 2013. Social competition and its consequences in female  
443 mammals. *J Zool.* 289(3):151-171.

444 Clutton-Brock TH, Parker GA. 1992. Potential reproductive rates and the operation of  
445 sexual selection. *Quart Rev Biol.* 67(4):437-456.

446 Dauphiné TC, McClure RL. 1974. Synchronous Mating in Canadian Barren-Ground  
447 Caribou. *J Wildl Manage.* 38(1):54-66.

448 de Jong K, Forsgren E, Sandvik H, Amundsen T. 2012. Measuring mating competition  
449 correctly: available evidence supports operational sex ratio theory. *Behav Ecol.*  
450 23(6):1170-1177.

- 451 de Jong K, Wacker S, Amundsen T, Forsgren E. 2009. Do operational sex ratio and  
452 density affect mating behaviour? An experiment on the two-spotted goby. *Anim*  
453 *Behav.* 78(5):1229-1238.
- 454 de Vos A, Brokx P, Geist V. 1967. A review of social behavior of the North American  
455 Cervids during the reproductive period. *Amer Midl Nat.* 77:390-417.
- 456 Denoël M, Hector MP, Poncin P. 2005. Courtship behavior in the Alpine newt *Triturus*  
457 *alpestris* at two different densities of males. *Herpetol.* 61:373-379.
- 458 Debuse VJ, Addison JT, Reynolds JD. 1999. The effects of sex ratio on sexual  
459 competition in the European lobster. *Anim Behav.* 58:973-981.
- 460 Dunbar RIM, Dunbar EP. 1977. Dominance and reproductive success among female  
461 gelada baboons. *Nat.* 266(5600):351-352. doi: 10.1038/266351a0
- 462 Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating  
463 systems. *Sci.* 197:215-223.
- 464 Espmark Y. 1964. Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Anim Behav.*  
465 12(1):159-160.
- 466 Forsgren E, Amundsen T, Borg AA, Bjelvenmark J. 2004. Unusually dynamic sex roles  
467 in a fish. *Nat.* 429(6991):551-554.
- 468 Geist V. 1999. *Deer of the world*. Shresbury, England: Swan Hill Press.
- 469 Grant JWA, Foam PE. 2002. Effect of operational sex ratio on female-female versus  
470 male-male competitive aggression. *Can J Zool.* 80(12):2242-2246.
- 471 Hardin DR, Warnick AC, Fields MJ. 1980. Artificial insemination of subtropical  
472 commercial beef cattle following synchronization with cloprostenol (ICI 80996):  
473 II estrous response. *Theriogen.* 14(4):259-268.
- 474 Head MK, Lindholm AK, Brooks R. 2008. Operational sex ratio and density do not  
475 affect directional selection on male sexual ornaments. *Evol.* 62(1):135-44.
- 476 Hirotani A. 1989. Social relationships of reindeer *Rangifer tarandus* during rut -  
477 implications for female choice. *Appl Anim Behav Sc.* 24(3):183-202.
- 478 Holand Ø, Weladji RB, Røed K. 2012. Shit happens – a glimpse into males' mating  
479 tactics in a polygynous ungulate - the reindeer. *Rang.* 32(1):65-71.
- 480 Horrocks J, Hunte W. 1983. Maternal rank and offspring rank in vervet monkeys: An  
481 appraisal of the mechanisms of rank acquisition. *Anim Behav.* 31(3):772-782.
- 482 Husband TP, Davis PB. 1984. Ecology and behavior of the Cretan agrimi. *Can J Zool.*  
483 62(3):411-420.



484 Iwasa Y, Odendaal F. 1984. A Theory on the Temporal Pattern of Operational Sex  
485 Ratio: The Active-Inactive Model (Vol. 65).

486 Janicke T, Morrow EH. 2018. Operational sex ratio predicts the opportunity and  
487 direction of sexual selection across animals. *Ecol Let.* 21(3):384-391.

488 Jirotkul M. 1999. Operational sex ratio influences female preference and male-male  
489 competition in guppies. *Anim Behav.* 58(2):287-294.

490 Johnson CT. 1978. Time to onset of oestrus after the injection of heifers with  
491 cloprostenol. *Vet Rec.* 103(10):204-206.

492 Johnstone RA, Reynolds JD, Deutsch JC. 1996. Mutual mate choice and sex differences  
493 in choosiness. *Evol.* 50(4):1382-1391.

494 Klemme I, Ylonen H, Eccard JA. 2007. Reproductive success of male bank voles  
495 (*Clethrionomys glareolus*): the effect of operational sex ratio and body size.  
496 *Behav Ecol Sociobiol.* 61(12):1911-1918.

497 Klug H, Heuschele J, Jennions MD, Kokko H. 2010. The mismeasurement of sexual  
498 selection. *J Evol Biol.* 23(3):447-462.

499 Kokko H, Monaghan P. 2001. Predicting the direction of sexual selection. *Ecol Let.*  
500 4(2):159-165.

501 Kokko H, Rankin DJ. 2006. Lonely hearts or sex in the city? Density-dependent effects  
502 in mating systems. *Phil Trans Roy Soc B-Biol Sc.* 361(1466):319-334. doi:  
503 10.1098/rstb.2005.1784

504 Krebs J, Davies N. 1987. *An Introduction to Behavioural Ecology*, 2nd ed. Sinauer  
505 Associates, Inc., Publishers, Sunderland, MA.

506 Krupa J, Sih A. 1993. Experimental studies on water strider mating dynamics: spatial  
507 variation in density and sex ratio. *Behav Ecol Sociobiol.* 33(2):107-120.

508 Kvarnemo C, Ahnesjo I. 1996. The dynamics of operational sex ratios and competition  
509 for mates. *Tr Ecol Evol.* 11(10):404-408.

510 Kvarnemo C, Forsgren E, Magnhagen C. 1995. Effects of sex ratio on intra- and inter-  
511 sexual behaviour in sand gobies. *Anim Behav.* 50:1455-1461.

512 L'Italien L, Weladji RB, Holand Ø, Røed KH, Nieminen M, Côté SD. 2012. Mating  
513 group size and stability in reindeer *Rangifer tarandus*: the effects of male  
514 characteristics, sex ratio and male age structure. *Ethol.* 118(8):783-792.

515 Lauer MJ, Sih A, Krupa JJ. 1996. Male density, female density and intersexual conflict  
516 in a stream-dwelling insect. *Anim Behav.* 52:929-939.

517 Martin P, Bateson P. 2007. Measuring behaviour: An introductory guide (Third ed.).  
518 Cambridge, UK: Cambridge University Press.

519 McEwan EH. 1963. Reproduction of barren ground caribou, *Rangifer tarandus*  
520 *groenlandicus* (Linneaus), with relation to migration. Doctor of Philosophy,  
521 McGill University, Montreal, Quebec.

522 McLain DK. 1992. Population density and the intensity of sexual selection on body  
523 length in spatially or temporally restricted natural populations of a seed bug.  
524 Behav Ecol Sociobiol. 30:347-356.

525 Melnycky NA, Weladji RB, Holand Ø, Nieminen M. 2013. Scaling of antler size in  
526 reindeer (*Rangifer tarandus*): sexual dimorphism and variability in resource  
527 allocation. J Mam. 94(6):1371-1379.

528 Milner JM, Nilsen EB, Andreassen HP. 2007. Demographic side effects of selective  
529 hunting in ungulates and carnivores. Cons Biol. 21(1):36-47.

530 Milner-Gulland EJ, Bukreeva OM, Coulson T, Lushchekina AA, Kholodova MV,  
531 Bekenov AB, Grachev IA. 2003. Conservation - Reproductive collapse in saiga  
532 antelope harems. Nat. 422(6928):135-135.

533 MSD Animal Health. 2013. Estrumate. Retrieved from [https://www.msd-animal-](https://www.msd-animal-health.co.nz/binaries/Estrumate_Website_Label_Mar_2013_tcm51-37026.pdf)  
534 [health.co.nz/binaries/Estrumate\\_Website\\_Label\\_Mar\\_2013\\_tcm51-37026.pdf](https://www.msd-animal-health.co.nz/binaries/Estrumate_Website_Label_Mar_2013_tcm51-37026.pdf)

535 Mysterud A, Holand Ø, Roed KH, Gjostein H, Kumpula J, Nieminen M. 2003. Effects  
536 of age, density and sex ratio on reproductive effort in male reindeer (*Rangifer*  
537 *tarandus*). J Zool. 261:341-344.

538 Odde KG. 1990. A review of the synchronization of estrus in postpartum cattle. J Anim  
539 Sc. 68:817-830.

540 Okuda N. 1999. Sex roles are not always reversed when the potential reproductive rate  
541 is higher in females. Am Nat. 153:540-548.

542 Pitnick S. 1993. Operational sex ratios and sperm limitation in populations of  
543 *Drosophila pachea*. Behav Ecol Sociobiol. 33(6):383-391.

544 Prins H, Iason G. 1989. *Dangerous Lions and Nonchalant Buffalo*. Behav.  
545 108(3/4):262-296.

546 R Core Team. 2017. R: A Language and Environment for Statistical Computing.  
547 Vienna, Austria: R Foundation for Statistical Computing. Retrieved from  
548 <https://www.R-project.org>

549 Raihani NJ, Grutter AS, Bshary R. 2010. Punishers Benefit From Third-Party  
550 Punishment in Fish. *Sc.* 327(5962):171.

551 Ropstad E, Kindahl H, Nilsen TAB, Forsberg M, Sire JE, Pedersen O. 1996. The effect  
552 of cloprostenol in non-pregnant and pregnant Norwegian semi-domestic reindeer  
553 (*Rangifer tarandus tarandus*). *Anim Rep Sc.* 29:1.

554 Rosvall KA. 2011. Intrasexual competition in females: evidence for sexual selection?  
555 *Behav Ecol.* 22(6):1131-1140.

556 Rowell JE, Shipka MP. 2009. Variation in gestation length among captive reindeer  
557 (*Rangifer tarandus tarandus*). *Theriogen.* 72(2):190-197.

558 Røed KH, Holand Ø, Smith ME, Gjøstein H, Kumpula J, Nieminen M. 2002.  
559 Reproductive success in reindeer males in a herd with varying sex ratio. *Mol*  
560 *Ecol.* 11:1239.

561 Sharp SP, Clutton-Brock TH. 2011. Competition, breeding success and ageing rates in  
562 female meerkats. *J Evol Biol.* 24(8):1756-1762. Skogland T. 1989. Comparative  
563 social organization of wild reindeer in relation to food, mates and predator  
564 avoidance. *Adv Ethol.* 29:1-77.

565 Smith CC, Sargent RC. 2007. Independent effects of male and female density on sexual  
566 harassment, female fitness, and male competition for mates in the western  
567 mosquitofish. *Behav Ecol Sociobiol.* 61:1349-1358.

568 Tennenhouse EM, Weladji RB, Holand Ø, Roed KH, Nieminen M. 2011. Mating group  
569 composition influences somatic costs and activity in rutting dominant male  
570 reindeer (*Rangifer tarandus*). *Behav Ecol Sociobiol.* 65(2):287-295.

571 Tennenhouse EM, Weladji RB, Holand Ø, Nieminen M. 2012. Timing of reproductive  
572 effort differs between young and old dominant male reindeer. *Ann Zool Fenn.*  
573 49(3):152-160.

574 Thiele J, Markussen B. 2012. Potential of GLMM in modelling invasive spread. *CAB*  
575 *Reviews Perspectives in Agriculture Veterinary Science Nutrition and Natural*  
576 *Resources.* 7:1-10.

577 Verrell PA, Krenz JD. 1998. Competition for mates in the mole salamander, *Ambystoma*  
578 *talpoideum*: tactics that may maximize male mating success. *Behav.* 135:121-  
579 138.

580 Wacker S, Mobley K, Forsgren E, Myhre LC, de Jong K, Amundsen T. 2013.  
581 Operational sex ratio but not density affects sexual selection in a fish. *Evol.*  
582 67(7):1937-1949.

583 Weir LK, Grant JWA, Hutchings JA. 2011. The Influence of Operational Sex Ratio on  
584 the Intensity of Competition for Mates. *Am Nat.* 177(2):167-176.

585 Weladji RB, Body G, Holand Ø, Meng XX, Nieminen M. 2017. Temporal variation in  
586 the operational sex ratio and male mating behaviours in reindeer (*Rangifer*  
587 *tarandus*). *Behav Proc.* 140:96-103.

588 Young A, Oosthuizen M, Lutermann H, Bennett N. 2010. Physiological suppression  
589 eases in Damaraland mole-rat societies when ecological constraints on dispersal  
590 are relaxed. *Hor Behav.* 57(2):177-83.

591 Zhang JJ, Zhang ZB. 2003. Influence of operational sex ratio and density on the  
592 copulatory behaviour and mating system of Brandt's vole *Microtus brandti*. *Acta*  
593 *Theriol.* 48(3):335-346.

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597 **Tables**

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

<b>Behaviour</b>	<b>Description</b>	<b>Codes</b>
Rest	Lying down, sleeping, or ruminating.	<b>R</b>
Stand	Standing and not showing any movement behaviour or foraging behaviour.	<b>S</b>
Walk	Slow movement.	<b>W</b>
Foraging	Eating behaviour.	<b>E</b>
Chase	Displace an individual and pursue that individual over time and space.	<b>C</b>
Herding	Perusing a female until she returns to the mating group.	<b>H</b>
Spar	Short bouts of locked antlers coupled with agonistic behaviours to determine social rank.	<b>SP</b>
Displace	One individual approaches another, and that individual retreats.	<b>D</b>
Court	Following a female or walking beside her while performing mating behaviours.	<b>CO</b>
Copulation attempt	Mounting without copulation.	<b>AC</b>
Copulation	Mounting with pelvic thrusting.	<b>COP</b>
Bush thrashing	The rubbing of antlers against shrubs or small flexible trees.	<b>BT</b>
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.	<b>SK</b>
Scent marking	Urination on hind legs.	<b>SM</b>

Head threat	Shaking of head to show off antlers (can lead to displacement).	<b>HT</b>
Grunting	A series of low sounding, husky, rapid rattles, which are brought about by frequent expirations of air.	<b>G</b>
Follow	Following an individual (behind them).	<b>FO</b>
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.	<b>FL</b>
Mate Guarding	Keeping other males away from a female. Following her, side by side.	<b>MG</b>

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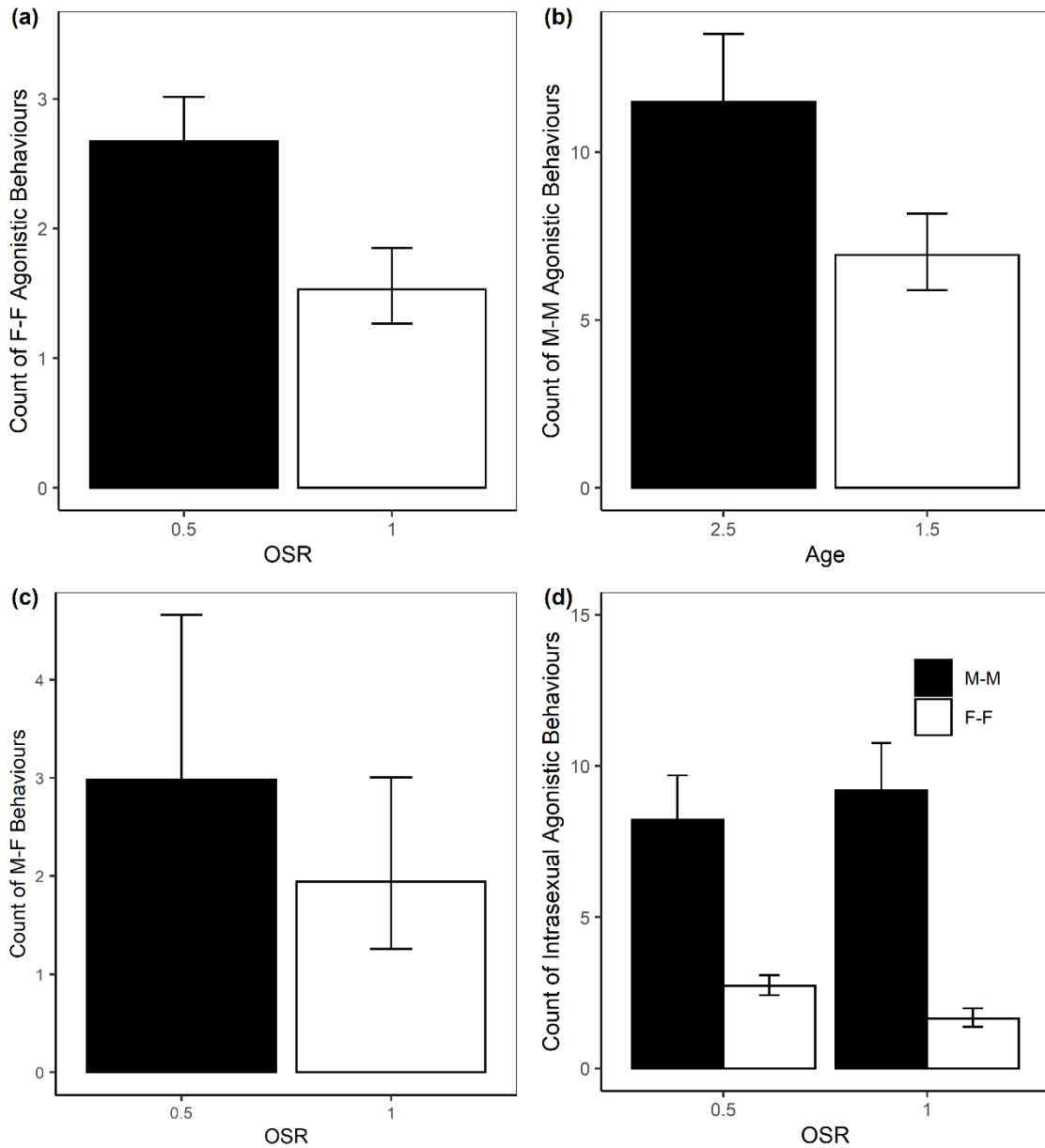
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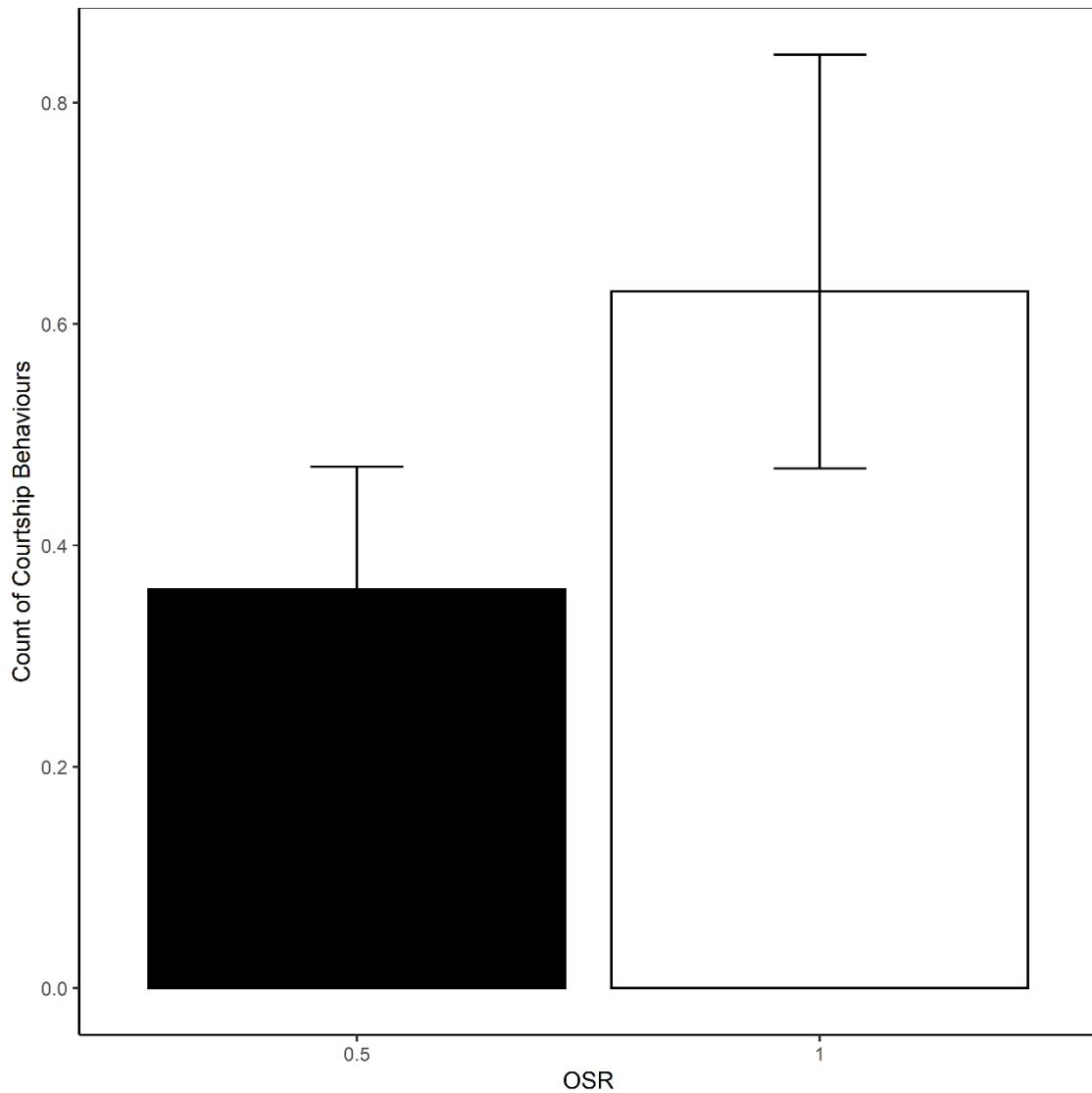
608 **Figures**



609

610 **Figure 1.** The negative-binomial linear model predictions for the average frequency of  
 611 occurrence (counts) of pooled agonistic behaviours (displacement, chase, spar, fight and  
 612 head threat) with the 95% confidence interval bars of male (1.5- or 2.5-year-old) or  
 613 female (mixed age) reindeer (*Rangifer tarandus*) between OSR treatments: (a) The  
 614 relationship between female-female (F-F) agonistics and OSR, independent of male  
 615 age, (b) The relationship between male-male (M-M) agonistics, and male age,  
 616 independent of OSR, (c) A comparison of male and female intersexual (M-F)  
 617 agonistics in relation to OSR, independent of male age, and (d) The relationship  
 618 between intrasexual agonistics and OSR, independent of male age.

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620

621 **Figure 2.** The negative-binomial linear model predictions for the average frequency of  
 622 occurrence (counts) of pooled courtship behaviours (attempted copulation, copulation,  
 623 mate guarding, follow, court, herd and flehmen) with the 95% confidence interval bars  
 624 of mixed age female and either 1.5- or 2.5-year-old male reindeer (*Rangifer tarandus*),  
 625 independent of OSR.

626



627 **Figure Captions**

628 **Figure 1.** The negative-binomial linear model predictions for the average frequency of  
629 occurrence (counts) of pooled agonistic behaviours (displacement, chase, spar, fight and  
630 head threat) with the 95% confidence interval bars of male (1.5- or 2.5-year-old) or  
631 female (mixed age) reindeer (*Rangifer tarandus*) between OSR treatments: (a) The  
632 relationship between female-female (F-F) agonistics and OSR, independent of male  
633 age, (b) The relationship between male-male (M-M) agonistics, and male age,  
634 independent of OSR, (c) A comparison of male and female intersexual (M-F)  
635 agonistics in relation to OSR, independent of male age, and (d) The relationship  
636 between intrasexual agonistics and OSR, independent of male age.

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640 **Figure 2.** The negative-binomial linear model predictions for the average frequency of  
641 occurrence (counts) of pooled courtship behaviours (attempted copulation, copulation,  
642 mate guarding, follow, court, herd and flehmen) with the 95% confidence interval bars  
643 of mixed age female and either 1.5- or 2.5-year-old male reindeer (*Rangifer tarandus*),  
644 independent of OSR.

645