1 **Temporal variation in the operational sex ratio and male mating behaviours**

2 **in reindeer (*Rangifer tarandus*)**

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20 **Running head:** Variation in males mating tactics with OSR

21   ABSTRACT

22   In polygynous species, sexual selection is mostly driven by male ability to monopolize access to

23   females in oestrous. In ungulates, the operational sex ratio (OSR), i.e. the proportion of males to

24   individuals ready to mate, varies throughout the peak rut, resulting from the temporal variation in

25   the number of females in oestrous. But the way males adjust their mating tactics to maximise

26   their access to females in oestrous (i.e. as OSR varies) is yet to be investigated. Using 15 years of

27   behavioural observations in reindeer (*Rangifer tarandus*), we compared the relative importance

28   of time within the rutting season (days to the peak-rut) and the OSR to explain the variation in

29   the propensity (i.e. the frequency after controlling for the potential number of encounters) of

30   young and adult dominant males to engage in four mating tactics: herding females, chasing other

31   males, investigating female reproductive status, and courting females. Male-male agonistic

32   behaviour was the most frequent mating behaviour, followed by herding. As predicted, dominant

33   male mating tactics changed over the rutting season: first herding, then chasing other males, and

34   finally investigating and courting females. In contrast to our prediction, we did not find support

35   for the OSR theory. We noted some discrepancies in how young and adult dominant males

36   adjusted their tactics during the mating season, adults being more efficient in timing and in

37   performing their behaviour to maximise access to females in oestrous. The reported sequence of

38   mating tactics may be more efficient than a static mating tactic to monopolize females in

39   oestrous, regardless of the population composition.

40

41   Keywords: courtship, intrasexual aggression, mating tactics, OSR, polygyny, ungulates

42

1. Introduction

Sexual selection, the driver of 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 for access to mates and from female mate choice (Darwin, 1871). In polygynous mammalian species, sexual selection is mostly driven by male ability to monopolize access to females in oestrous (Emlen and Oring, 1977). Accordingly, male mating tactics vary with the temporal and spatial distribution of females in oestrous, as well as male ability to control female movement (Clutton-Brock, 1989). Classical mating systems theory predicts that a male's ability to monopolize females in oestrous, and therefore the strength of sexual selection, increases with the level of competition, best measured by the operational sex ratio (OSR), i.e. the proportion of males to the total number of individuals ready to mate (de Jong et al., 2012). However, male ability to monopolize females in oestrous may depend on how mates are acquired (Klug et al., 2010). To increase their ability to monopolize females, dominant males may devote more time and energy into mating behaviours, especially when the competition is stronger i.e. higher OSR (Emlen and Oring, 1977), but also when there are more females to defend (lower OSR); which will in turn influence their mating success (Coltman et al., 1998; Pelletier and Festa-Bianchet, 2006; Willisch et al., 2012).

When female oestrus is short and highly synchronous, such as in ungulates (de Vos et al., 1967), the number of females in oestrous is expected to follow an inverse U-shaped curve, with many females in oestrous during the peak-rut period, and few during the early and late rut periods (Hirotani, 1989). Accordingly, and as the number of mature males remains constant within a single rut season in closed populations, the OSR will exhibit a U-shaped pattern, with a minimum during the peak rut. OSR theory would therefore predict a U-shape curve of male

66   investment in competitive behaviour over the rut: low aggression during the peak rut and higher

67   aggression early and late in the season.

68   An alternative to the prediction made from the OSR theory is that males adjust their tactics

69   according to time in the rutting season (early, peak, and late rut), independently of the level of

70   competition. The plasticity of ungulate male mating tactic is well documented (e.g., Carranza et

71   al. 1995; Pelletier, 2005) among species, populations, years and individuals (de Vos et al., 1967;

72   Carranza, 2000; Brockmann, 2001; Mysterud et al., 2004; Isvaran, 2005). Male ungulates adjust

73   their reproductive effort to the phenology of females in oestrous (Mysterud et al., 2008) and we

74   can therefore expect them to also adjust their mating tactic, especially in regards to their

75   influence on their reproductive success. Behaviours which have an indirect benefit (e.g. herding

76   – pursuing a female until she returns to the mating group; or male-male aggressions – either

77   chasing other males from the mating group or fighting to maintain the dominance) are useless

78   toward the end of the rut, while those which have an immediate benefit (such as investigating

79   females – to assess their reproductive status and find the female currently in oestrous;   or

80   courting females – following a female while performing mating displays) are useless at the

81   beginning of the rut.

82   We used 15 years of rutting behaviour data to study the phenology of male mating tactics and

83   their variation with OSR in reindeer *Rangifer tarandus*. Reindeer has a short mating season with

84   most females copulating within 10 days (Kojola, 1986; Skogland, 1989) and females have a short

85   oestrus (Espmark, 1964; Hirotani, 1989; Ropstad, 2000), inducing a strong temporal variation of

86   the OSR. Male reindeer mating tactics have been suggested to be particularly flexible (Clutton-

87   Brock, 1989), and males adjust their reproductive effort to local conditions, such as group size

88   and number of competitors (Tennenhouse et al., 2011). Male age has a strong influence on the

89 timing of reproductive effort (Mysterud et al., 2004; Tennenhouse et al., 2012) and also

90 influences the efficiency of male mating behaviours (L'Italien et al., 2012; Body et al., 2014).

91 Accordingly, we tested the following three predictions, the first one being associated to the

92 phenological hypothesis, the second being associated to the OSR hypothesis, and the third one

93 related to the influence of age on the reported patterns: (1) Dominant male mating tactics will

94 change with the time during the rutting season, in the following order; (a) herding females at the

95 beginning of the rut, (b) investigate and copulate with females mostly during the peak-rut and

96 then (c) court females at the end of the peak rut. We also expect inter-male agonistic behaviours

97 to increase during the peak rut. (2) Males will spend more time into each of these mating

98 behaviours with an increase in OSR, particularly for the inter-male agonistic behaviours. (3) We

99 further predicted that the expected pattern will be more pronounced for adult dominant males as

100 compared to juvenile, less experienced dominant males.

101

102 **2. Methods**

103 *2.1.Study area and study population*

104 The study was conducted at the Kutuharju Field Reindeer Research Station, in Kaamanen,

105 Finland (69°N, 27°E). We collected data from a semi-domestic Reindeer population free ranging

106 in two large fenced areas: the southeast Sinioivi (13.4 km²) and the northwest Laulavaara (13.8

107 km²). Birch *Betula spp* and Pine *Pinus sylvestris* forests, boggy areas and lakes characterized the

108 enclosures. The herd composition (a herd is the population in an enclosure in a particular year)

109 was experimentally modified every year for 15 years (1996 to 2011 except 1998) for a total of 16

110 enclosure-years (Table 1). We changed the number of males and females, and therefore the adult

111 sex ratio, as well as the male age structure, i.e. only young, only adult or mixed age structure

112   (Table 1). Apart from these experimental herd compositions, animals were free ranging within

113   enclosure limits and behaved naturally. Males were fitted with VHF radio collars while females

114   were fitted with coloured collars, both with unique identification facilitating mating group

115   composition determination and the monitoring of individual behaviour. Using Lent (1965)'s

116   definition of a group, a mating group (also called harem) was considered "*an aggregation of*

117   *individuals separated by some distance from other aggregations, showing coordination of*

118   *activities, such as travelling together or resting and feeding together*", with at least one male and

119   one female (Uccheddu et al. 2015). Because individuals had ear tags, we could track their

120   identity through years (34% of the males were present two or more years). Every day from mid-

121   September to mid-October we located collared males and their harem using ground tracking, and

122   recorded group composition (number of males and females and their identities) and behaviours

123   of dominant males, i.e. harem holders which are easily identified in *Rangifer*. Indeed, every time

124   we found a group the dominant male was clearly recognised, occupying a central position,

125   contrary to the satellites, and performing mating behaviours more than any other male (typically

126   chasing other males, grunting, or herding females; see Tennenhouse et al. 2011 for details on

127   dominant males determination) and independently of their age.

128

129   *2.2.The operational sex ratio (OSR)*

130   We defined the OSR as the proportion of males to the total number of individuals ready to

131   mate, i.e. mature males and females in oestrous (de Jong et al., 2012). We calculated the OSR on

132   a daily basis at the herd level (OSR herd$_{day}$) and at the group level (OSR$_{group}$). The number of

133   males ready to mate is defined as the number of mature males in the herd or as the number of

134   mature males in a given group. We estimated the number of females in oestrous in the herd or in

135 a given group on a daily basis using a backdating procedure from birth date and three calculation

136 steps as presented below, assuming that females were in oestrous for a single day. Oestrus

137 duration has been estimated to last between 24 h and 48 h in reindeer (Espmark, 1964; Hirotani,

138 1989; Ropstad, 2000).

139 First, we estimated the mating day of every female that gave birth in each herd. We removed

140 from their birth date the gestation duration controlled for the age of the female, the sex of the calf

141 and the mating time (Eq. 1, Mysterud et al., 2009; coefficients were provided by Atle Mysterud,

142 personal communication). For further analyses, we excluded very late mating dates, i.e. which

143 occurred in November or later, as they may more likely represent a second oestrus cycle.

144 Equation 1

$$Mating\ date = \frac{Birth\ date - 282.83 - 1.65 \times Sex - 0.31 \times Age + 365}{-0.23 + 1}$$

145 Where *Mating date* and *Birth date* are in Julian days (January first = 1); *Sex* is calf sex (Male =
146 1; Female = 0); *Age* is the age of the mother when she gave birth.
147
148 Second, we estimated the statistical density of females in oestrous from the histogram

149 distribution of mating days in each herd separately. Then, we multiplied this density by the

150 number of females in the herd to obtain the expected value of the number of females in oestrous

151 in a herd at a given date (*Oestrous herd$_{day}$*). We calculated the number of females in oestrous in a

152 group at a given date (*Oestrous group$_i$*) based on the proportion of the mature females of the herd

153 present in the group (Equation 2).

154 Equation 2

$$Oestrous\ group_i = Oestrous\ herd_{day} \times \frac{females\ group_i}{females_{herd}}$$

155 Where *Oestrous group$_i$* and *Oestrous herd$_{day}$* is the number of females in a given group i or on a
156 given day in the herd, respectively; *females group$_i$* and *females$_{herd}$* are the number of females in a
157 given group i and in the herd, respectively.

158

159   By doing so, we made two assumptions. First, we assumed that unmated or females that

160   aborted had a similar temporal distribution of their oestrus as compared to females that gave

161   birth. Second, we assumed females in oestrous were equally distributed among mating groups.

162   Although these assumptions may be violated as youngest females are the least likely to give birth

163   and mate later (Eloranta and Nieminen, 1986; Skogland, 1989), and as females in oestrous may

164   group around particular males more than anoestrous females, i.e. female mate choice, it is the

165   most parsimonious assumption to estimate oestrus day of females that did not give birth and their

166   distribution among groups.

167   Third, we calculated the OSR as the proportion of mature males to the total number of

168   individuals ready to mate (i.e. mature males + females in oestrous), daily at the herd level

169   (Equation 3), and for each group (Equation 4). We calculated the operational sex ratio at the herd

170   level on a daily basis (OSR_{herd}) and the operational sex ratio at the group level (OSR_{group}).

171

172   Equation 3

$$OSR\ herd_{day} = \frac{males_{herd}}{males_{herd} + Oestrous\ herd_{day}}$$

173   Equation 4

$$OSR\ group_i = \frac{males\ group_i}{males\ group_i + Oestrous\ group_i}$$

174   Where OSR $herd_{day}$ and OSR $group_i$ are the operational sex ratio in the herd a given day and in a
175   given group, respectively; $males_{herd}$ and males $group_i$ the number of males in the herd and in a
176   given group, respectively; *Oestrous herd$_{day}$* and *Oestrous group$_i$* the number of females in
177   oestrous in the herd a given day or in a given group, respectively.

178

179   *2.3. Timing of the mating season*

180   To compare mating seasons, we centered each one on its median mate date (defined as Julian

181   Day: JD = 0). The peak-rut week was defined as the week surrounding this date and only used

182   for descriptive purpose. We centered OSR values as well as behavioural records. We analyzed

183   the data recorded during the month surrounding the median mate date (i.e. from JD = -14 to JD =

184   14) as the probability a female was in oestrous was too low before that period and to avoid an

185   overlap with a potential second peak-rut, as female reindeer can re-ovulate if they were not

186   fertilized in their first oestrus. We also reported every copulation observed while in the field.

187   These records were centered as described above, and we only displayed those who are in the

188   time interval of interest.

189

190   *2.4.Dominant male mating tactics*

191   Dominant male mating behaviour was observed based on the focal observation technique

192   (Martin and Bateson, 2007). We observed the dominant male for 15 minutes. Every 15 seconds,

193   we recorded the activity of the dominant male (rest, feed, stand, and walk) as well as his mating

194   behaviours. Behavioural frequencies were divided by the focal duration to estimate the

195   proportion of time spent performing an activity. Focals on the dominant male started when he

196   was active (i.e. not resting) and were not performed more frequently than one focal per hour. We

197   tried to observe every dominant male each day, but only males with the highest status were able

198   to remain dominant in a group throughout the mating season. Dominant males, independently of

199   their age, were observed and the data analysed. Subdominant satellites males were also observed,

200   but the corresponding data was not analysed or included in this study.

201   We summed the proportion of time dominant males spent in particular mating behaviours to

202   define four groups of behaviours representing four *tactics* : *Agonistic* corresponds to inter-male

203   competition through agonistic behaviours (Display, Spar, Fight, Displace, Chase); *Herd*

204 corresponds to male attempt to control female movements (Herd, Chase females ; see Espmark

205 1964 for description) ; *Investigate* corresponds to males' assessment of a female reproductive

206 status and the copulation attempts that may result (it includes Flehmen, Investigate, Sniff,

207 Attempt copulation) ; *Court* corresponds to males mating behaviours which denote male

208 spending time close to a female seeking her attention in the hope of obtaining her agreement to

209 mate with her (Court, Follow female; see de Vos et al., 1967 and Tennenhouse et al. 2012 for

210 description).

211

212 *2.5. Statistical analysis*

213 We assessed the influence of the operational sex ratio of a group (OSR_{group}) and the time of

214 the rut on time dominant males spent in the mating tactics using, for each tactic taken separately,

215 a generalized additive mixed model (GAMM) fitted with a logistic link function and binomial

216 error structure, weighted by the focal duration, and using males identity as random factor

217 (intercept only). We fitted the effect of OSR_{group} as linear and quadratic effect (Tennenhouse et

218 al., 2011), and the time of the rut using a smoothing parameter ($k = 4$). A smoothing parameter of

219 4 was chosen after visual inspection of the temporal patterns obtained.

220 The frequency of mating behaviour is influenced by the potential for this activity, i.e. the

221 number of encounters with a partner/competitor, and by the propensity for this activity, i.e. the

222 likelihood the dominant male will perform the activity at a given encounter (de Jong et al.,

223 2012). We therefore introduced a term to control for the potential of each activity. The potential

224 for *Agonistic* mating behaviour was defined as the number of competitors in the group, i.e. the

225 number of males minus one; the potential for *Herd* and *Investigate* mating behaviours were the

226 number of females in the group; and the potential for *Court* was the number of females in

227   oestrous in the group, i.e. *Oestrous group$_i$*, as males do not court anoestrous females, while they

228   herd and investigate all females. The number of encounters in a group may be non-linearly

229   related to the number of partners or competitors present in the group, so we fitted the term

230   *Potential* both as linear and quadratic.

231   The age of the dominant male has a strong effect on his behaviour and the timing of his

232   mating effort (see introduction). Consequently, each of the above variables was introduced in the

233   model with an interaction with the age of the dominant male, which is a categorical variable:

234   Young < 3 years old (hereafter "young dominant males"); and Adult > 3 years old (hereafter "old

235   dominant males"). The full model is therefore given by equation 5:

236   Equation 5

$$Behaviour = Age + Potential + Potential{:}Age + \ Potential^2 + Potential^2{:}Age$$
$$+ \ OSR_{group} + OSR_{group}{:}Age + \ OSR^2_{group} + OSR^2_{group}{:}Age + Time$$
$$+ Time{:}Age$$

237 Where *Behaviour* is the proportion of time spent in a given mating tactic; *Potential* is the number
238 of individuals with which the dominant male can interact to perform the mating behaviour; *Time*
239 is the time of the rut centered on the median mate date; *Age* is the age of the dominant male
240 (young or adult). Interactions are represented by ":".
241
242   We adopted an all subset approach (Symonds and Moussalli, 2010), and therefore we fitted

243   all of the simpler models derived from the above full model with some conditions. First, if one

244   variable is fitted as a quadratic term, *Age* interacts with either both terms (i.e., *X:Age + X²:Age*)

245   or none (i.e., *X+X²+Age*). Second, *Age* always interacts with *Time* if time is in the equation.

246   Third, *Age* and *Potential* are always in the equation. Finally, we tested for both quadratic effect

247   and linear effect for the variables *Potential* and *OSR$_{group}$*. We chose the best model according to

248   the corrected Akaïke Information Criterion (AICc). We retained the most parsimonious model

249 among the competing models that differed in AICc by less than 2 (Burnham and Anderson,

250 2002). All statistical analyses were performed using R 3.0.3 (R, 2011).

251 From the proportion of deviance explained by the retained model, we calculated the

252 proportion of the explained deviance which is explained by the variables *Potential*, the OSR_{group}

253 and the *Time*. To do this, we calculated the ratio of proportion of deviance explained by the

254 retained model without one of these variables (and their interaction with *Age*) to the proportion

255 of deviance explained by the retained model.

256

257 **3. Results**

258 *3.1. Operational sex ratio (OSR), the timing of mating seasons*

259 We recorded 843 calf birth between May 2nd and August 8th (82.9% of the females gave birth

260 during that period; others were either slaughtered or did not give birth, Table 1). We excluded 57

261 calf birth date from further analyses as they were likely resulting from the second oestrus

262 (corresponding to fertilization occurring in November or later). The estimated median mating

263 date varied between October 1st and October 17th (Table 1). The operational sex ratio at the herd

264 level (OSR_{herd}) varied greatly among years (Fig 1a), and on average OSR_{herd} initially decreased

265 and then increased during the peak-rut week for each year taken separately (Fig 1). The OSR_{group}

266 varied greatly (average $\pm$ sd = 0.79 $\pm$ 0.16) from a female biased situation (minimum OSR_{group} =

267 0.289) to a highly male biased situation (maximal OSR_{group} = 0.995). We observed 222

268 copulations within the two weeks surrounding the estimated mid-peak rut (Fig 1b). These

269 observations are not totally synchronized with the estimated mid-peak rut, as copulations were

270 observed, on average, 1.5 days after the mid-peak rut. This difference is certainly due to a bias in

271 our ability to observe early copulations in the field.

272

3.2. Dominant male mating tactics

We recorded 1122 focal observations of dominant males, for a total of 276 hours of observation. These records came from the observation of 75 different dominant males (median number of observation per individual = 8). Mating group composition ranged from 1 to 70 females (average ± sd = 14.3 ± 11.5 females), and from 1 to 18 males (average ± sd = 2.6 ± 2.7 males). We recorded focal observations from 441 young dominant males and 681 adult dominant males. Young dominant males faced competitors in their group in 182 focal observations, while adult dominant males faced competitors in 353 focal observations.

Dominant males spent on average 2.5% ± 5.4 of their time performing the mating behaviours analysed in this study, the rest of their time being dedicated to standing, eating, walking and resting. Dominant males spent most of that time in inter-male agonistic behaviours (49.7%), then herding females (26.4%), investigating female reproductive status (15.3%), and courting was the least performed mating tactic (8.4%).

286

3.3. Selected models

The full model best explained the variability of the time spent in agonistic mating tactics with no competing models. It included the effect of the number of competitors and its quadratic term, the effect of the OSR_{group} and its quadratic term, the effect of time, and the interaction of each of these variables with the age of the dominant male (Table 2). The model explained 6.9% of the deviance.

The selected model to explain the variability of the time spent herding females was in competition with two other models ($\Delta AICc$ = +0.4 for the retained model). It included the effect

295 of the number of females, its quadratic term and their interactions with the age of the dominant

296 male, the effect of the OSR_{group} and the effect of time within the rutting season and its interaction

297 with the age of the dominant male (Table 2). The model explained 5.1% of the deviance.

298   The selected model to explain the variability of the time spent investigating females had no

299 competing model. It included the effect of the number of females, the effect of the OSR_{group} as

300 quadratic term, the effect of time and the interaction of all of those variables with the age of the

301 dominant male (Table 2). The model explained 8.3% of the deviance.

302   The selected model to best explain the variability of the time spent courting females included

303 the effect of the number of females in oestrous, the effect of the OSR_{group} as quadratic term, the

304 effect of time, and the interactions of all of those variables with the age of the dominant male

305 (Table 2) The model explained 6.3% of the deviance.

306

307 *3.4. Influence of the potential number of encounters, the OSR and the time*

308   For both young and old dominant males, we found the potential number of encounters to

309 have a quadratic relationship with the proportion of time spent in agonistic behaviours (Fig 2a;

310 increasing and then decreasing when more than 9 males are present) and herding (Fig 2b;

311 increasing and then decreasing when more than 22 females are present). As for the time spent

312 investigating females and courting females in oestrous, the relationship with the number of

313 individuals was positive for adult dominant males, but negative for young dominant males (Fig

314 2cd).

315   In general, for both young and adult dominant males, an increase of the competition among

316 males (i.e. increasing OSR_{group}) negatively influenced the propensity of males to engage into all

317 mating related behaviours (Fig 3abc). At the highest OSR_{group} ($OSR_{group} > 0.8$), however, young

318 dominant males engaged more in agonistic behaviours (Fig 3a), and adult dominant males

319 engaged more in investigating and courting behaviours (Fig 3cd). We observed no influence of

320 OSR_{group} on the propensity of young dominant males to engage in courting behaviours (Fig 3d).

321   The different mating tactics were displayed at different time during the rut (Fig 4). Both

322 adult and young dominant males were mostly involved in agonistic behaviours at the end of the

323 peak-rut (Fig 4a). They mostly herded females at the beginning of the peak rut (Fig 4b), and they

324 mostly investigated female reproductive status (Fig 4c) and courted them (Fig 4d) at the end of

325 the peak-rut. The temporal pattern of mating behaviour is less marked for young dominant males

326 than for adult dominant males (Fig 4e).

327   As displayed in Table 3, the potential number of encounters accounted for most of the

328 deviance explained by the inter-male agonistic mating tactic model (62.5%; Table 3). The

329 OSR_{group} accounted for a large portion of the deviance explained for the investigating and the

330 courting mating tactics (27.8%, 24.1%, respectively; Table 3). The time within the rutting season

331 accounted for a large part of the deviance explained by the models related to the three female

332 directed mating tactics (Herd 42.8%; Investigate: 33.8%; Court 43.5%; Table 3).

333

334 **4. Discussion**

335   Our result clearly supported the idea that OSR in ungulates vary throughout the peak rut

336 time, thereby validating the assumption under which we based our predictions. We found indeed

337 that OSR varies for our population both within years, and among years during the study period,

338 being at its smallest values around the mid-peak rutting time. Our results also appeared to show

339 that OSR is not the main predictor of males mating tactics, and that its relation with the

340 propensity of males to engage in mating behaviours is complex.

341

4.1 Timing of the rutting season

We found that male reindeer clearly displayed a variety of mating tactics, supporting previous reports that most animals (Gross, 1996; Roff, 1996; Oliveira et al., 2008; Neff and Svensson, 2013), including ungulates (Isvaran, 2005; Pintus et al., 2015), are flexible in their mating tactics. More importantly, and in accord with our prediction, we found a sequence in dominant male mating tactics: males were first herding at the beginning of the peak rut week. During the peak rut, dominant males mostly chased other males, as this behaviour is mainly influenced by the number of subdominant males available to chase, which is highest during the peak rut. At the end of the peak-rut, dominant males were mostly investigating and courting females. This sequence appeared to match with a strategy that maximizes access to females in oestrous and thereby optimizing individual reproductive success (Isvaran, 2005; Pintus et al., 2015). In a fission-fusion group dynamics system, using a single tactic may not be optimal. Groups are so unstable that harem defense alone is not sufficient, group movements are not spatially predictable and often groups are moving on a too large area to adopt a resource-defense or a lek mating tactics. Moreover, females' oestrus can be so synchronous that a tending mating tactic would secure too few females. Males herd females before the peak rut to ensure they control a large enough mating group during the peak rut. Also, males tend to defend mating groups during the peak-rut, when herding is less required – as enlarging groups at the end of the peak rut is less beneficial, justifying the tendency for group stability to decrease (Body et al., 2015). At the end of the peak rut, a harem defense tactic is costly and risky (as the group may split and females in oestrous may occur by chance in the sub-group leaving), and so it is more efficient for males to use a tending tactic, which is more expected when females are spread out or

364   when they form groups too large to be defended (Emlen and Oring, 1977; Clutton-Brock, 1989;

365   Carranza, 2000; Isvaran, 2005). In conclusion, we can state that instead of an array of mating

366   tactics, reindeer males use a sequence of mating tactics: herding, then chasing, and finally

367   tending (investigating and courting). It is to be expected that this sequence is stable across years,

368   as it will increase male mating opportunities independently of the males-females ratio. Such a

369   sequence of mating tactics seems appropriate for fission-fusion group dynamics systems. Indeed,

370   alternative mating tactics are selected to maximize fitness, leading to the suggestion that such

371   plasticity in mating tactics might represent the adaptive adjustment of the males' behaviours to

372   differences in social and environmental conditions (Emlen and Oring, 1977; Clutton-Brock,

373   1989; Carranza, 2000).

374

375   4.2 Male ability to perform mating behaviours

376   Our study showed that both young and adult dominant males displayed the above mentioned

377   sequence of mating behaviours. Most discussions of alternative mating tactics in ungulates have

378   looked at populations with a mixed male age structure within a group, most of them showing that

379   adult males tend to monopolize females while younger males usually adopt sneaking tactics

380   (Roed et al., 2002; Willisch et al., 2012; Pintus et al., 2015). Here we show that young dominant

381   males also display mating behaviours often attributed to adult males, such as herding, and in the

382   similar sequence. Alternative mating tactics are therefore a second choice for young males, and

383   they will display harem-defense and tending mating behaviours if given the opportunity.

384   However, we noted some discrepancies in how young and adult dominant males performed

385   them.

386   Both young and adult males display a limit to their herding ability. Males start decreasing

387   their time spent herding when there are more than 22 females to control. Herding is so costly for

388   males reindeer that it may be uneconomical to keep herding while competing with other males at

389   the same time (Brown, 1964; Tennenhouse et al., 2011). Young and adult dominant males

390   herding behaviour therefore do not differ in their propensity to engage into this behaviour, but

391   rather in their timing, young males being unable to match it at the beginning of the peak rut, and

392   to its outcome. Moreover, young males are not efficient at herding females back to the group

393   surely due to their inexperience. Earlier studies in this population suggested already adult

394   dominant males to be more efficient in herding females, and holding larger and more stable

395   mating groups (Holand et al., 2006; Tennenhouse et al., 2011; L'Italien et al., 2012; Body et al.,

396   2014).

397   Males also display a limit to their propensity to engage into inter-male agonistic behaviour,

398   and this limit is influenced by their age. Adult dominant males spent less time chasing other

399   males when they were more than 9 other males in the group, while this limit is dropped to 4 other

400   males for young dominant males. There is also a strong difference between adult and young

401   dominant males in their interactions with females: as expected, adult dominant males spent more

402   time investigating and courting females when there were more females in oestrous, as compared

403   to young dominant males. These results are in agreement with other finding, showing that many

404   aspects of male reproduction, such as duration of male-male aggression (Jennings et al., 2004)

405   and copulatory success (Apollonio et al., 1992) are affected by experience.

406   The sequence of mating tactics is also less pronounced for young dominant males than for

407   adult dominant males, mostly for herding and courting behaviours. There is evidence that large

408   males can time their reproductive effort to coincide more precisely with female ovulation than

409   small males (Preston et al., 2003; Meise et al., 2014). Adult male savannah baboons (*Papio*

410   *cynocephalus*) appear to compete more intensely for females on the two most likely days of

411   conception (Bercovitch, 1988). All these may again be attributed to experience, and it is clear

412   that adult dominant males are more efficient in timing their reproductive effort (e.g. adult

413   dominant males only spent a small proportion of time investigating) in order to achieve higher

414   reproductive success as compared to young dominant males (Willisch and Ingold, 2007; Willisch

415   and Neuhaus, 2009; Tennenhouse et al., 2012; Willisch et al., 2012; Pintus et al., 2015).

416

5. Conclusions

418   Here we have shown that OSR varies through the rut, because of the number of female in

419   oestrous changing with time. We also reported that the level of competition, as measured by the

420   OSR, is not the main driver of male mating behaviours. To monopolize more females in

421   oestrous, dominant males adjust their mating behaviours in relation to the time of the rut, and the

422   social environment. It clearly appeared indeed that young and adult dominant males performed

423   the same ritual when it comes to mating behaviours, following the same sequence: herding,

424   agonistic, investigating and courting. Adult males were however more efficient in timing their

425   effort and performing these mating behaviours than young males, which may explain their ability

426   to monopolize most oestrous female. Our study confirms that reindeer mating strategy is highly

427   flexible, and points to a more complex relationship between mating behaviours and mating

428   success, suggesting that intrasexual variation in mating tactics in relation to time may be

429   adaptive. It also improves our understanding of the mechanism through which dominant males

430   achieve higher reproductive success.

431

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555 **Tables**

556 Table 1. Herds compositions (number of females, number of males, and male age structure), calf
557 production (number of calf produced from September or October mating in the herd, and in
558 bracket the calves produced from mating occurring late and therefore excluded from the
559 analysis), the estimated mid-peak rut date (median mate date) and sampling effort (number of
560 focals)

Year	Enclosure	Females	Males	Males age	Calves (excluded)	Peak-rut	Sampling effort
1996	Lauluvaara	46	6	Young	27 (3)	14th Oct	119
1997	Lauluvaara	47	5	Young	37 (7)	13th Oct	63
1997	Sinioivi	47	18	Mixed	38 (6)	9th Oct	70
1999	Sinioivi	75	3	Adult	48 (10)	16th Oct	107
2000	Sinioivi	74	3	Young	53 (9)	17th Oct	67
2001	Sinioivi	79	11	Young	63 (4)	7th Oct	47
2002	Sinioivi	92	4	Mixed	81 (4)	2[sd] Oct	72
2003	Sinioivi	52	4	Mixed	44 (4)	8th Oct	104
2004	Sinioivi	48	5	Mixed	44 (0)	5th Oct	51
2005	Sinioivi	55	17	Mixed	39 (2)	6th Oct	64
2006	Sinioivi	80	19	Mixed	67 (1)	1st Oct	84
2007	Sinioivi	87	24	Mixed	70 (4)	6th Oct	83
2008	Sinioivi	41	12	Mixed	31 (1)	1st Oct	57
2009	Sinioivi	42	17	Mixed	39 (0)	1st Oct	16
2010	Sinioivi	75	24	Mixed	59 (0)	1st Oct	59
2011	Sinioivi	34	11	Mixed	23 (0)	1st Oct	59

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Table 2. Model selection based on AIC to explain the variability of the four mating tactics (agonistic, herd, investigate females, court). We
present all the models within ΔAICc ≤ 2 or the two models with the lowest AIC if there were only one model within ΔAICc ≤ 2. Bold terms
correspond to selected models. An ":" means "interaction". The age of the dominant male and the potential were always included, and the
interaction between time and age was always included if the time variable was included in the model

Model	Age	Potential	Potential^2	Potential : Age	OSR	OSR^2	OSR : Age	Time : Age	AICc	ΔAICc
Agonistic										
1	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**3040.7**	**0**
2	x	x	x	x	x	x		x	3049.0	8.3
Herd										
1	x	x	x	x	x		x	x	1946.3	0
2	**x**	**x**	**x**		**x**			**x**	**1946.7**	**0.4**
3	x	x	x	x	x			x	1947.6	1.3
Investigate										
1	**x**	**x**		**x**	**x**	**x**	**x**	**x**	**1372.1**	**0**
2	x	x	x	x	x	x	x	x	1374.6	2.57
Court										
1	**x**	**x**		**x**	**x**	**x**	**x**	**x**	**1374.9**	**0**
2	x	x	x	x	x	x	x	x	1378.9	4.08

568 Table 3. Proportion (in percent) of the deviance explained by selected models for each mating
569 tactic and proportion (in percent) of that explained deviance which can only be explained by
570 the potential number of encounters, the OSR_{group} or the time, with their interaction with the
571 age of the dominant male if included in the model

Mating tactics	Deviance explained by selected models	Proportion of deviance only explained by		
		Potential	OSR_{group}	Time
Agonistic	20.5	62.5	11.8	12.6
Herd	9.99	5.0	4.0	42.8
Investigate	12.6	34.2	27.8	33.8
Court	17.8	32.3	24.1	43.5

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Figures captions

Figure 1. Variation of (a) the herds' operational sex ratio, and (b) the distribution of the observed copulations throughout the rut. Each year is centered on their estimated median mating date (time = day 0) based on the backdating procedure, and the shaded bar corresponds to the peak-rut week. In (a), solid lines are Lauluvaara herds and dashed lines are Sinioivi herds. The color of the line is proportional to the year of study (darkest = 1996; lightest = 2011)
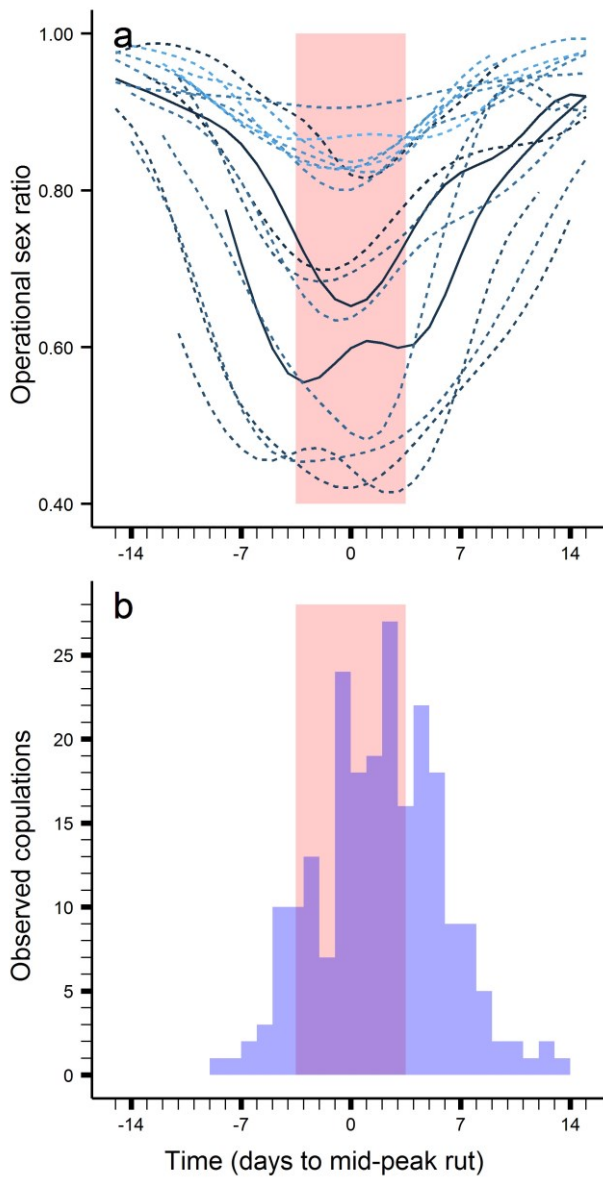
Figure 2. Influence of the potential number of encounters on the proportion of time spent in each mating tactics by young (left panels) and adult (right panels) dominant males. The potential number of encounters correspond to the number of competitors in the group for (a) the inter male agonistic mating tactic, the number of females in the group for (b) the herding mating tactic, and for (c) the investigating mating tactic, and it corresponds to the number of females in oestrous for (d) the courting mating tactic. Partial effect (solid line) and their 95% confident intervals (grey area) were calculated using the median OSR_{group} (OSR_{group} = 0.48) and at October 1st (time = 0). Dots correspond to partial residuals averaged (a) per competitor, (b,c) per 5 females, and (d) per 0.25 females in oestrous. Dot sizes are proportional to the number of data. Top and diagonal numbers on each panel indicate the actual value of the matching point which is outside the display range of the y axis

Figure 3. Influence of the operational sex ratio in the group (OSR_{group}) on the proportion of time spent in each mating tactics (a: inter male agonistic mating tactic; b: herding mating tactic; c: investigating mating tactic; d: courting mating tactic) by young (left panels) and adult (right panels) dominant males. Partial effect (solid line) and their 95% confident intervals (grey area) were calculated using the median potential number of encounters per age class (Competitor: 1/1; Females: 9/13; Females in oestrous: 0.31/0.48; for young/adult dominant males) and at October 1st (time = 0). The dots correspond to partial residuals averaged per 0.05 unit of OSR_{group}. Dot sizes are proportional to the number of data. Top and diagonal numbers on each panel indicate the actual value of the matching point which is outside the display range of the y axis

Figure 4. Influence of the time of the rut (centered on the peak rut date: time = 0) on the proportion of time spent in each mating tactics (a: inter male agonistic mating tactic; b: herding mating tactic; c: investigating mating tactic; d: courting mating tactic) by young (left panels) and adult (right panels) dominant males. Partial effect (solid line) and their 95% confident intervals (grey area) were calculated using the median potential number of encounters per age class (see Fig 2), and the median OSR_{group} (see Fig 3). The dots correspond to partial residuals averaged per day. Dot sizes are proportional to the number of data. Top and diagonal numbers on each panel indicate the actual value of the matching point which is outside the display range of the y axis. To best compare the timing of each mating tactics, we display (e) the scaled variation of the predictions made on each mating tactic: inter male agonistic behaviour (black solid line), herding behaviour (black dotted line), investigating behaviour (grey solid line), courting behaviour (grey dashed line). The pink bars correspond to the peak-rut week
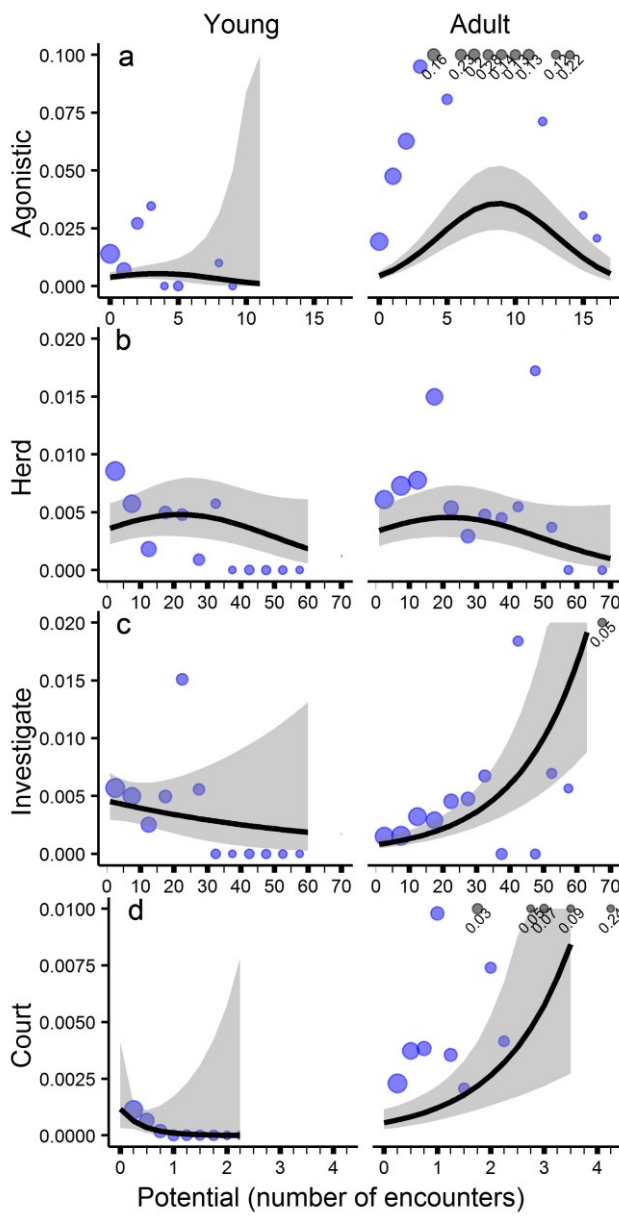
617   Figure 1
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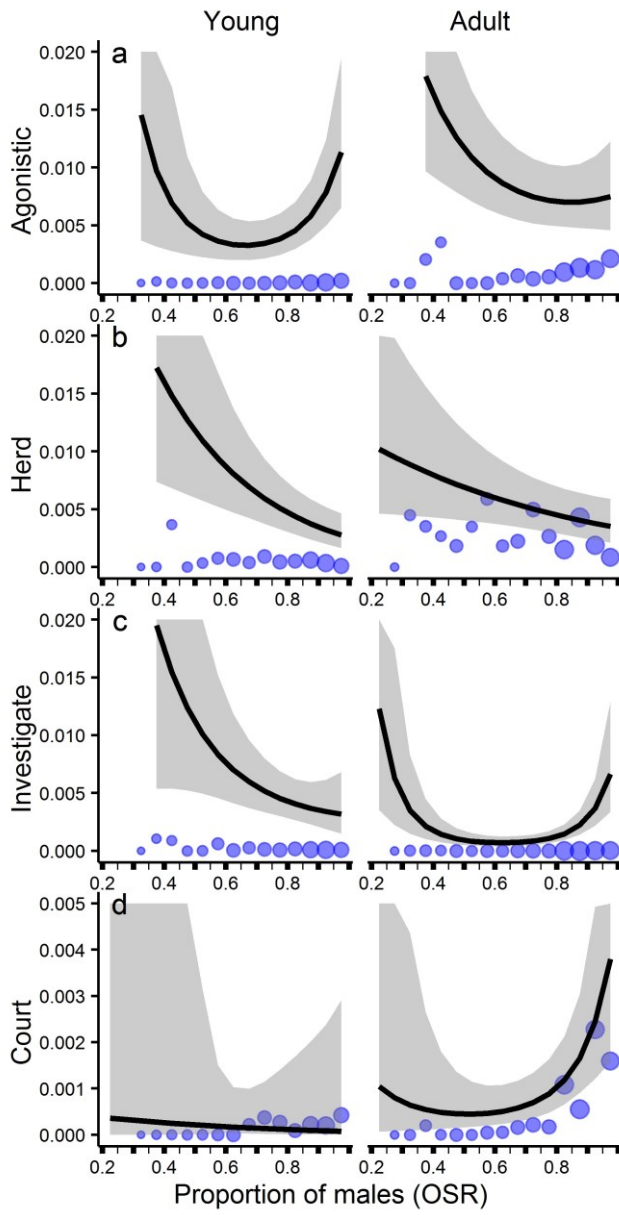619
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Figure 2

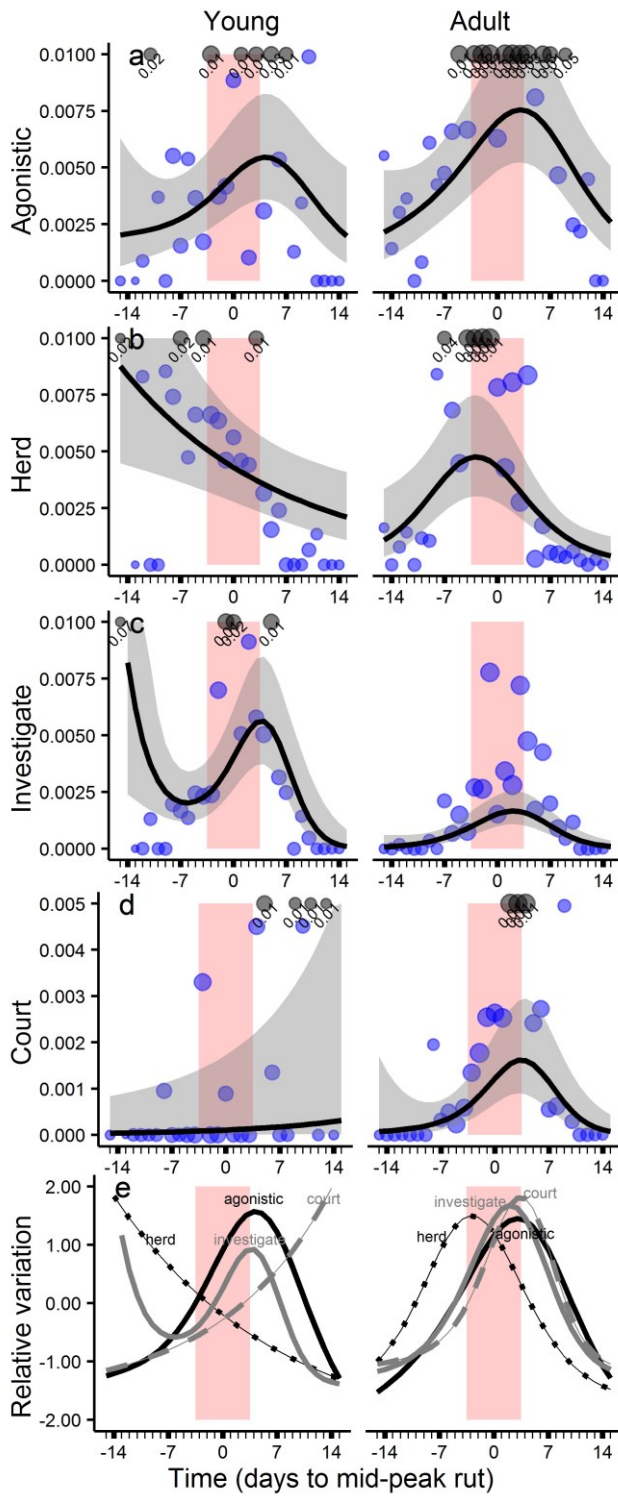625   Figure 3
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