

Field article

Shit happens – a glimpse into males' mating tactics in a polygynous ungulate - the reindeer

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Abstract: This is about the two big "guys", Spot and Mika, and their endeavour to propagate their genes during the mating season 2007. They were 6 and 5 years old weighting 172 and 141 kg before rut, respectively. Together with 23 other males (one 5 yrs, two 4 yrs, three 3 yrs, six 2 yrs and eleven 1 yr old) they roamed within a ~15 km² fenced area competing for access to 87 females. Indeed, the competition was intense and all males present contributed to the dynamic observed. Especially Hot, the heaviest 4 yrs old male weighing 155 kg before rut, played a prominent role – in addition to Spot and Mika, their mating tactics being highly dynamic. However there is no short cut to success – strength have to be coupled with smartness - but shit happens - as we'll see.

Key words: intrasexual selection; male-male combats; mating tactics; reindeer; reindeer male mating strategy, videos.

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Rivalry

Prelude - Spot's early rise

Spot started rutting early (Photo 1). Already in mid September he started to show off; herding females as well as chasing rivals while grunting confidently. Towards the end of September his rutting activity steadily intensified (Fig.1a), controlling a growing mating group (Fig. 1c). This coincided with his first mating attempt (Fig. 2), suggesting that the females were starting to come into heat. Controlling such a

big female group always on the move searching for food, while 10-15 other males were hanging around waiting for their chance, took all his attention. Indeed, Spot traded feeding with keeping control as confirmed by the strong inverse relationship between alert standing and foraging.

Mika (Photo 2) showed a different prelude. His tolerance towards other males and limited herding behaviour kept spending low and left more time available for foraging (Fig. 1b). As a consequence,



Photo 1. Spot with some ladies. Photo: Natasa Djaković.



Photo 2. Mika. Photo: Léon L'Italien.



Photo 3. Spot & Hot fighting. Photo: Léon L'Italien.

his pre rut mating group was small as compared to Spot's (Fig. 1c). Most of the other prime- (4 & 5 yrs) and semi prime-aged (3 yrs) males were also actively trying to form mating groups, as opposed to the youngsters (1 and 2 yrs old males), but their groups were labile.

The beat is on

Spot's intolerance towards rivals climaxed October 2nd as the herd entered the peak rut (2nd – 9th October). Especially the inexperienced 1 yr old males were vigorously chased by Spot as they eagerly and optimistically approached "his" females. Mika who joined Spot's group October 1st, kept a low profile (Fig. 1). He was watching the "ballgame" carefully, burning as little fuel as possible and hoping for the "jackpot" – to take over the whole mating group now consisting of around 50 females (Fig. 1c), of which many were starting coming into oestrus.

Spot was vigilantly standing watching and grunting (Fig. 1a) and at the same time eagerly chasing rivals and herding as well as inspecting females. However, his intense mating behaviour created unease among the females. They spread out to mitigate the annoyance. This seriously stretched his controlling capacity. We could actually "feel" that his body reserves were shrinking. Indeed, his tactic paid off as confirmed by several successful copulations observed the first days of October (Fig. 2). But, would Spot be able to keep up his pace through the peak rut? If not, who would enter the centre court? Or would the big mating group start to disintegrate?

Hot enters the scene - Mika - the "smarty" - takes control
October 3rd in the early afternoon Hot suddenly arrived together with a small group of females and took on Mika who was operating in the outskirts of Spot's group, right away (click for video 1). Hot put up a tough fight but finally gave in and ran away. However, fifteen minutes later he returned - fit for a fight - and challenged Spot, the big boss (Photo 3) (click for video 2). After seven minutes fighting bravely Hot had to throw in the towel. Immediately, Mika fresh after the warming up round with Hot 20 minutes earlier, challenged Spot, still punch-drunk, and knocked him out after a short (two minutes) intense fight (click for video 3).

In the evening the dust had settled. Mika was in control of the big mating group, now consisting of 65 females. In addition, 16 rivals were swarming around. October 4th Spot was able to keep a small mating group of around 15 females, whereas the rest (~40) stayed with Mika (Fig. 1c). The next day the two groups had merged again (Fig. 1c). Spot stayed in the outskirts. His collapse seemed complete and his tactic shifted accordingly; hanging around to see what happens. Actually, he started foraging (Fig. 1b) and tried to get going. Hot also returned - still "hot" -, but was effectively controlled by Mika. He had learned his lesson and stayed in the periphery of the group for the rest of the peak rut.

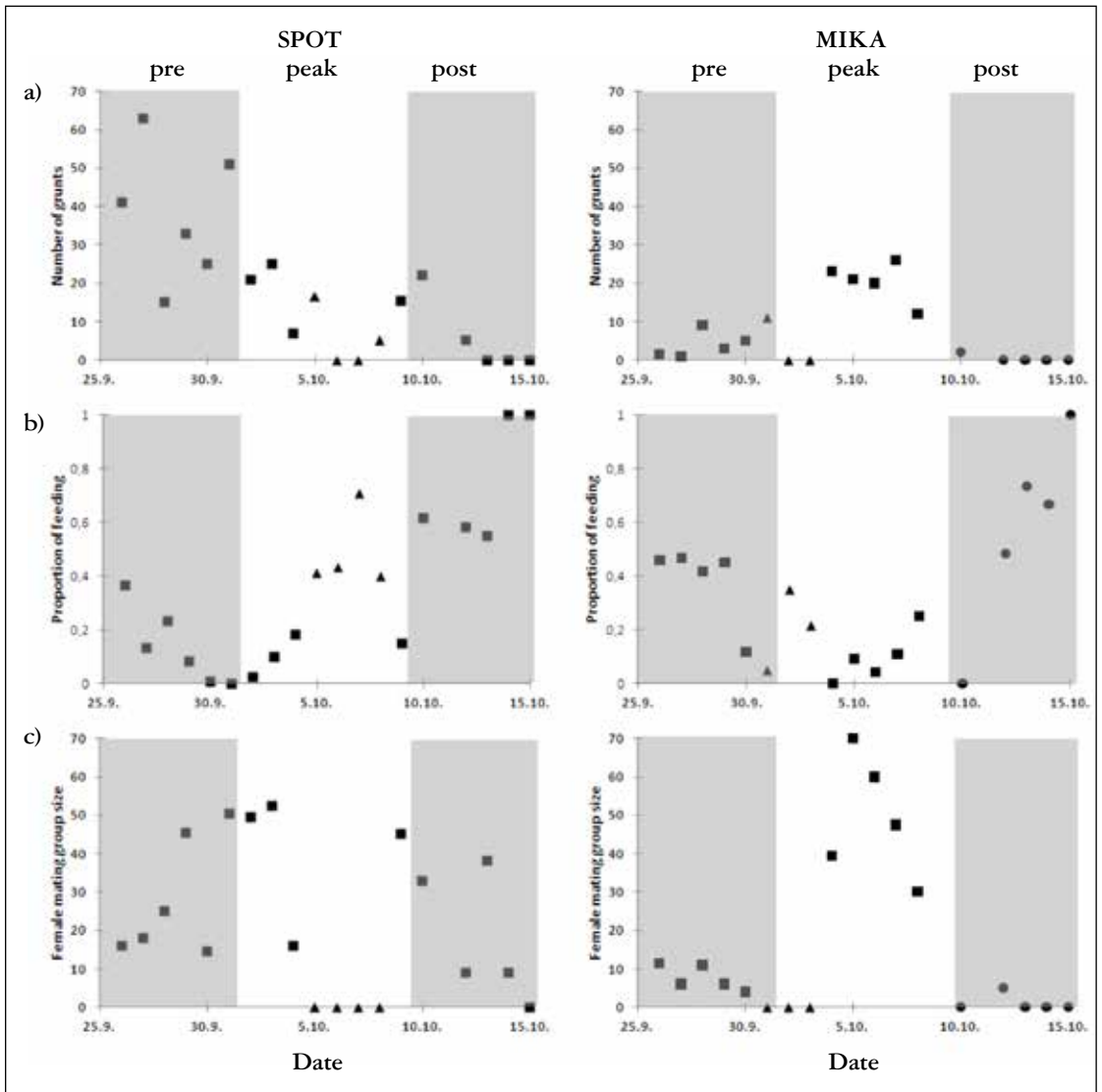


Fig. 1. Daily average; grunting activity based on 5 minutes continuous observations (a) and proportion spent feeding (b) based on 15 minutes focals with observations every 15 seconds and female mating group size (the dominant male is given the score of all females within the group) (c) of Spot and Mika during pre (gray), peak (white) and post (gray) rut. Squares represent dominance within a mating group, triangles subdominance, whereas circles denote Mika being seriously injured.

Mika's beydays

Mika looked confidently subduing his rivals, apparently controlling them without burning too much fuel. The reduced chasing behaviour, as compared to Spot, seemed to calm down the females in the group and they were able to forage and rest undisturbed. Some of the young males tried to take on females in the outskirts of the mating group but they seemed to prefer to stay with Mika and moved towards the

centre when harassed. This eased his herding effort as he could patrol a rather condensed female group.

Although the females were rather calm and Mika acted confidently, it was impossible for him to defend such a big mobile group from intruding males. Hence, Mika displayed a mixed tactic, trying to keep the females tight by being tolerant towards rivals and herding the females gently and at the same time keeping a special eye on the female within the group

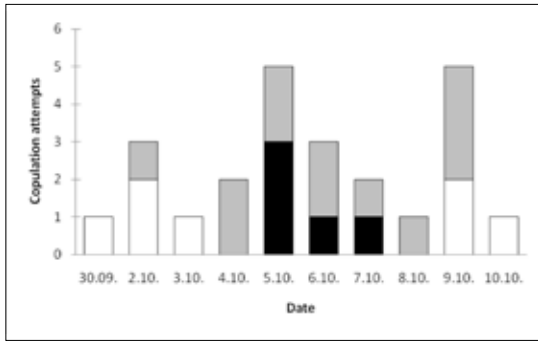


Fig. 2. Dates of observed copulation attempts by Spot (white), Mika (black) and other males (gray) in the main mating group.

closest to receptiveness. He actually let other prime and semi-prime males take part in the “vorspiel”. When the female approached receptiveness Mika interfered, took over the tending and courtshipping and copulated her. After mission completed, he lost interest and sought new females coming into heat.

Game over for Mika

October 7th we observed Mika limping. The day after we found him seriously affected (click for video 4). He was not able to put any weight on his left front leg. The injury made him less mobile and constrained his ability to express his superiority, as reflected in his decreased rutting behaviour (Fig. 1a) and reduced mating group size (Fig. 1c). It was only a matter of time before he would be overthrown, as also indicated by the increased rutting behaviour of his rivals. October 9th we found Mika alone – resting. The next day he was seen together with 5 females (Fig. 1c), not capable of following them as they moved on, and he was left behind.

Spot's Indian summer

Spot appeared like a bird Phoenix, as seen by his increased grunting activity from 8th to 9th October (Fig. 1a). He had obviously used his “time out” efficiently, foraging (Fig. 1b) and resting and had recuperated. But, his pace was tuned down as the herd was entering the post rut period (October 10th-15th) (Fig. 1a). Indeed, this seemed to be the case for all the prime and semi-prime males. They had lost most of their reserves compared to the youngsters, which still were in pretty good shape still eagerly checking females. The latest copulation attempt observed was October 10th (Fig. 2). Obviously there was little left to fight for and the big mating group started to disintegrate (Fig. 1c). Indeed, males' focus shifted and was

tuned towards charging their batteries (i.e. foraging) (Fig. 1b) before the onset of winter.

Reflections

The winner doesn't take it all

Based on the number of successful copulations seen and the mating group dynamic observed, Spot and Mika obviously seemed to be the two most successful males, as they alternated to dominate the main group consisting of around 50 females (Fig. 1c) during peak rut. Spot and Mika were equally successful, siring 15 and 14 offspring, respectively (Fig. 3). Thus the number of days of primacy and the mating group size during peak rut reflected their success, as also reported in other polygynous species (Pemberton *et al.*, 1992; Wade & Shuster, 2004). Nevertheless they fertilized only around 60% of the females in the main group, suggesting that some of the ~15 males hanging around also got their share.

Timing of the effort

The highly synchronised female ovulation in reindeer, about 90% of the copulation attempts were observed October 2nd – 9th (Fig. 2), induces strong selection pressure for timing males' reproduction effort, including their fighting ability, with females' reproductive phenology, as reported in other northern ungulates (Preston *et al.*, 2001; Myrsterud *et al.*, 2008). Indeed, all prime- and semi prime-aged males were at their top during peak rut, although some of them started their mating behaviour earlier than others and behaved differently. As reindeer females are receptive only one to two days (Ropstad, 2000), the operational sex ratio (OSR), defined as the ratio of fertile males to receptive females, during the peak rut period (October 2nd – 9th), will average about five times the absolute sex ratio. Given that the females distribute randomly between mating groups, irrespectively of their reproductive phase, the local (within group) OSR will be equally skewed during peak rut period, inducing intense local male-male competition.

A flexible strategy

The males alternated between different tactics based on local spatial and temporal variation in OSR and own status, as seen in many ungulates (reviewed by Isvaran, 2005). Indeed, the female oestrus asynchrony and the length of the receptiveness “window” seem sufficient to keep up the environmental potential for polygyny (Emlen & Oring, 1977) in reindeer. By keeping the females tight and defending them from intruders, the dominant male within a mating groups was “prepping” the females collectively. Actually also

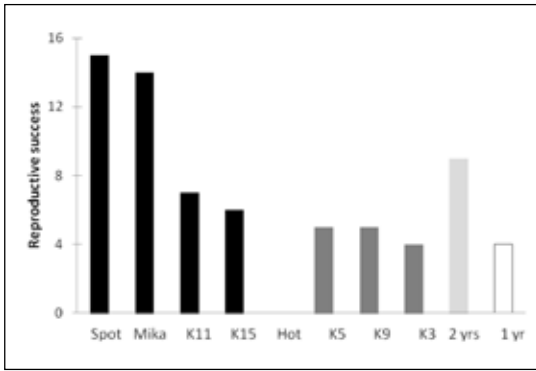


Fig. 3. Individual reproductive success of all prime (6, 5 & 4 yrs old, black) and semi-prime (3 yrs old, dark gray) males and collectively success for the 2 (light gray) and 1 (white) yrs old males, respectively.

his rivals contributed to the pre-courtship and got their share. The dominant males tried to keep the servicing time low (normally 2-4 hrs during peak rut) to be ready to seek for new receptive females within their group asap. The females, on the other hand, may be eager to extend the servicing time to reassure that the dominant male is the right guy. A longer servicing time will also reduce other females access to him and hence induce female-female competition for high quality males. This may actually explain some of the spread in reproductive success among males which affiliated with the main group during peak rut (Fig. 3). Indeed, mate competition and female choice do interact (Bro-Jørgensen, 2011), as seen by the female interest in Mika (click for video 4).

Sneaking – an age specific tactic

Given the intense local male-male competition during peak rut, Spot and Mikka focused primarily on controlling the most potent rivals, paying less attention to the youngsters although they were often targeted and chased as they dared to move rather freely within the mating group. This actually enabled most (four) of the 2 yrs and some (three) of the 1 yr old males staying mainly in the main group during peak rut to sneak around and “bush” mate a few (one, two or three) females each, adding up to 13 calves totally (Fig. 3). A similar pattern has also been reported by Røed *et al.* (2002). Obviously, to father calves at an early age gives an extra fitness bonus and induces age specific selective pressure to adopt a sneaking tactic when young as they were not able to form and control own groups in this highly competitive environment. However, in environments with only young (1 yr)

males available they may shift to a dominant tactic, although their herding ability and display is not fully developed (Holand *et al.*, 2006).

Conditional and condition dependent strategy

Also the three semi prime males (K9, K5 & K3) operated mainly within the main group and practised an alternative tactic; standing watching, trying to form temporal groups or herd off single females close to oestrus, siring 14 calves totally (Fig. 3). Hot was the big loser with no sire at all. He was watched intensively and taken “out” by Mika and Spot, alternatively, as soon as he approached an oestrus female. Hence, we didn’t observe any copulation attempt by him. Two of the prime age males (K11 and K15) formed small mating groups of their own during most of the peak rut and sired 7 and 6 calves, respectively (Fig. 3). Indeed, reproductive success is partly related to mating tactic, which is highly dynamic, both temporally and spatially, also among prime males.

Mika - the “smarty”

Mika’s tactic, staying around the main group and waiting for the big chance, did pay off as seen by the abrupt shift in dominance between Spot and Mika (Fig. 1), Hot being the catalysator. Indeed, to be successful males need experience; i.e. correct assessment of own condition and rivals strength combined with optimal timing and allocation of their limited resources. The “testosterone runaway” tactic practised by Hot seemed not adaptive, but he probably learned his lesson. Mika showed his experience also when in charge of the group. He adjusted his tactic according to male-male competition and female availability by combining group defence with tending individual females. Using his rivals as his extended “nose” and allowing them to take part in the “vorspiel”, Mika probably reduced his servicing time per female and hence increased his access to receptive females.

Body mass - not the only key to success

Males’ rank is clearly related to their body mass in polygynous ungulates (Clutton-Brock *et al.*, 1988), including reindeer (Espmark, 1964; Røed *et al.*, 2002). As males’ dominance within a mating group gives priority of access (Clutton-Brock *et al.*, 1982), the linear fit between body mass and reproductive success ($R^2 = 0.56$) is expected. The oldest male, Spot was 6 years, and the strong linear fit between age and success ($R^2 = 0.73$) suggests that none of the males had reach senescence. Building up and maintaining a big and powerful body is demanding. Indeed, males’ body mass reflects physical maturity and their capacity to take active part in the rut. As somatic effort

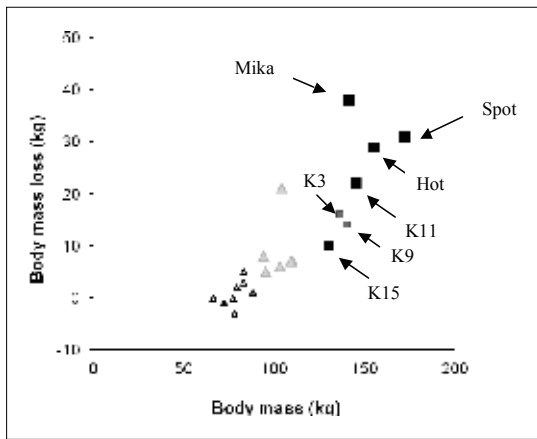


Fig. 4. Reproductive effort measured as body mass loss among males during the rut (September 6th - October 22nd) vs initial body mass (September 6th). Prime (6, 5 & 4 yrs old; black big squares.) semi-primed (3 yrs old; dark gray small squares, no body mass of K5 before rut), 2 yrs (light gray, big triangles) and 1 yr old males (white, small triangles). Missing values for one 3 yrs and one 1 yr old male.

increases with body mass (Fig. 4), the positive linear relationship between effort (i.e. absolute somatic loss) or relative effort (absolute losses/body mass) and reproductive success follows ($R^2 = 0.55$ and $R^2 = 0.43$, respectively). However, age specific analyses revealed no such relationship among young, nor among semi prime males (but only two males were available). Only among the prime-aged males we found a positive relationship, although rather weak ($R^2 = 0.21$). But, big guys and spenders can be losers. Hot put much effort and fighting spirit into the rut but did not get any output. During his life span (he was slaughtered after the rut 2007) Hot actually never sired any offspring – could he be sterile? Anyway, he played a vital role in the male dynamic. Excluding Hot from the analyses the positive effort - success relationship among prime males improved considerably ($R^2 = 0.79$).

Control is expensive

The strong linear negative relationship between time spent standing alert and eating for Spot and Mika during rut ($R^2 = 0.68$) suggests that they traded reduced energy intake with staying alert and keeping control, in line with the foraging constraint hypothesis (Pelletier *et al.*, 2009). In comparison, the 1 yr old males spent 66% foraging. As a consequence they were able to keep up their body mass during rut, only

losing 1 kg on average (Fig. 4). Indeed, their sneaking tactic seems not to involve any big effort, whereas the semi prime- and prime-aged males' tactic, being sub-dominant within the main group trying to "chop off" single or small groups of females, was pretty demanding (Fig. 4), as also confirmed by their increase time standing alert and reduced foraging activity.

High stake - big risk

The ultimate goal for a prime male is to control as big a group of females as possible during peak rut. Supremacy, and hence priority of access to females within a mating group is manifested through dominance behaviour. Indeed, fights are the ultimate expression of assessing competitive abilities among prime males. Although prime males' combats per se seem to contribute a minor part of their direct reproductive spendings, fights may lead to severe injuries among polygynous ungulates (Geist, 1986). Mikka's left foot was actually tangled in his own antlers when fighting off Hot (seen at the end of video 1, just after Hot ran away). Probably he got a cut which led to a serious infection and his resignation in late part of peak rut. Indeed, the winner may pay his toll.

Conclusion

Reindeer male mating strategy is highly fluid. We have identified four main (reversible) tactics; 1) Dominant; controlling as big a group as possible and willing to take the risks including fights to keep control as seen by Spot and Mika. While controlling the group, tending individuals females within the group coming into oestrus. 2) Wannabe; includes prime males willing to hang around as subdominants and wait for the chance to take over mating groups by fights, as seen by Spot, Mika and Hot. While waiting for the chance they practise the butcher tactic (see next point). 3) Butcher (Satellite); trying to chop off and isolate small female groups (from the main group) or single females as seen by the semi prime males (K9, K5 & K3). 4) Sneaker; an age specific tactic, used by young male not able to keep groups or tend individual females at high male-male competition.

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Video shooting

Videos are shot by Léon L'Italien and Anne Lene Hovland.

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Appendix 1

Methodology

The study was carried out at Kuthuharju Reindeer Research Station (69°N, 27°E) in northern Finland, 2007. Before rut the herd was rounded up and all animals were weighted (September 6th). All males (except seven 1 yr old) were fitted with radio collars, whereas the rest of the herd were equipped with numbered collars making individual identification possible. Blood was drawn from all animals. The experimental herd was released onto the rutting ground September 8th.

We tracked as many as possible mating groups (i.e. aggregates consisting of at least one female with at least one male present) daily from September 16th to October 15th, giving priority to the prime and semi-prime males. All animals associated with each group were recorded and the dominant male assessed based on observed rutting behaviour and agonistic interactions between males. We recorded males' activity (i.e. resting, walking, standing alert and eating) and direct rutting behaviour (i.e. flehmen, tripping back-legs while urinating, rubbing antlers, investigating females, tending, courtshipping, chasing and fighting rivals and herding females) every 15 seconds for 15 minutes based on the focal animal technique (Martin & Bateson, 2007). All focal observation periods containing the activity class rest were omitted. In addition, males vocalization (number of grunts) over a 5 minutes period was recorded at the end of the focal observation period, as a measure of excitement

level and hence the intensity of the rut. The dominant male within the group was the first to be chosen for focal observation. Thereafter subordinate male(s) present was (were) chosen. The dominant male within a group could actually be observed several times during a day. We here report average values of daily observations.

All copulation attempts, defined as mounting for at least 2 seconds were recorded. Consecutive copulation attempts of the same female by the same male within the same day were counted as one attempt. Further the rut was divided into pre, peak and post rut. Peak rut was defined as the shortest period where at least 90 % of all copulation attempts were observed. Actually 22 out of totally 24 copulation attempts in the main mating group were observed during peak rut (October 2nd – 9th) (Fig. 2). The pre rut and post rut were defined as one week prior to and the six days after peak rut, respectively.

The herd was again rounded up October 20th and all animals weighted (October 22nd) before released to their winter range. Eleven elderly females were slaughtered in October and December 2007 and two died during the following winter. Prior to calving in 2008 the females were rounded up and confined to a smaller calving area. Just after calving the calves were weighted and blood samples drawn for paternity analyses using microsatellite markers (Røed *et al.*, 2002). Four females did not give birth. Altogether 70 calves were sampled and 69 assigned to one of the males.