Flexible mating tactics and associated reproductive effort during the rutting season in male reindeer (*Rangifer tarandus*, L. 1758)

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Abstract   Polygynous males can change their mating tactics across their lifetime, but information is scarce on the flexibility of this trait within a given season and the relative costs and benefits of using different tactics. Here, we monitored individually marked male reindeer *Rangifer tarandus* and classified their mating tactics as harem-defense, sneaking, or mixed. The costs of the male reproductive effort were assessed using both direct (i.e. percentage of body mass lost) and indirect measures (i.e. activity patterns such as feeding, standing, and walking), while mating group size and reproductive success were recorded as mating effort benefits. Our results show that reindeer males may switch between the harem-defense and sneaking tactics throughout the same breeding season, providing further support to the notion that reproductive tactics are flexible in ungulates. The costs and benefits of male mating effort vary according to the mating tactic, reaching the highest values in harem-holders and the lowest values in sneaking males. Moreover, males who switched between the sneaking tactic and the harem-defence tactic tended to achieve higher mating success than males who consistently used the least costly tactic. Indeed, all harem-holders successfully sired offspring, whereas only two out of three mixed-tactic males sired one calf, and sneaking males did not sire any calves. In conclusion, our results show that reindeer males can modulate their mating efforts during the same breeding season by switching between the most costly harem-defense tactic and the least costly sneaking tactic, suggesting individual solutions to the balance between reproductive effort and mating opportunities [*Current Zoology* 61 (5): 802–810, 2015].

Keywords   Alternative mating tactics, Intraspecific variation, Phenotypic flexibility, Polygynous ungulate, Sexual behaviour

Across the animal kingdom, reproductive tactics are extraordinarily diverse both between and within species (Oliveira et al., 2008). Among mammals, ungulates show a remarkable intraspecific variation in male mating tactics (Isvaran, 2005), including harem-defense (Clutton-Brock et al., 1982), territory defense (Carranza et al., 1990), and lekking (Isvaran and Jhala, 2000). Harem-defense consists of monopolizing access to females and defending them against competitors, while less competitive males may stay close to the harem trying to sneak copulations (Espmark, 1964; Røed et al. 2002). Sneaking behaviour is therefore regarded as the alternative reproductive tactic of harem-defense (Wolff, 2008).

Alternative reproductive tactics refer to discontinuous behavioural and other traits selected to maximize fitness in two or more alternative ways in the context of intraspecific and intrasexual reproductive competition (Taborsky et al., 2008). Male mating tactics in ungulates are highly flexible and influenced both by internal (e.g. age, body mass, and body condition) and external (e.g. population density, sex-ratio, male age structure, and predation) factors (Isvaran, 2005). For instance, age and strength strongly affect mating tactic election, with mature prime-aged males monopolizing females, while young males usually adopt a sneaking tactic (Røed et al.,

2002; Willisch and Neuhaus, 2009; Willisch et al., 2012). Various tactics might indeed be used by the same individual throughout their lifetime, or even within the same breeding season (Wolff, 2008). Such a reversible within-individual variation, also known as phenotypic flexibility, is a function of internal or external conditions varying predictably or stochastically (Piersma and Drent, 2003; Isvaran, 2005). Flexible tactics might therefore represent the adaptive adjustment of the individual behaviour to the changing conditions (e.g. food distribution: Carranza, 2000; population density: Yoccoz et al., 2002; Mysterud et al., 2004; weather: Apollonio et al., 2013) in order to optimise male reproductive success. Nevertheless, the costs and benefits associated with each mating tactic are still poorly investigated (Isvaran, 2005).

In the present study we aimed to evaluate male mating effort in reindeer (*Rangifer tarandus*, Linnaeus 1758) as a function of individual traits and mating tactics. Reindeer are a strongly polygynous species with a mating season restricted to a few weeks during autumn when animals form temporary rutting or mating groups (Røed et al., 2002). Similar to other ungulates which have adapted to extreme environments and with limited resources, reindeer are capital breeders, meaning that they rely on stored reserves to face the outstanding reproductive effort (Stearns, 1992). Owing to their short mating season and their high reproductive investment, mating tactic election might play a crucial role in determining male reproductive success in this species. Several studies have focused on factors affecting mating effort in male reindeer (e.g. age and body mass: Kojola, 1991; age, density, and sex-ratio: Mysterud et al., 2003; mating group composition: Tennenhouse et al., 2011; age- and time-specific patterns in dominant males: Tennenhouse et al., 2012), but the role played by mating tactics is still largely unknown. Given that male ungulates rarely adopt only one tactic during the breeding season and during their lifetime (McElligott and Hayden, 2000; Isvaran, 2005; Willisch and Neuhaus, 2009), we hypothesised that not only do reindeer males behave as harem-holders or sneakers, but they may also switch between these two tactics within the same rutting season. Additionally, we were interested in measuring the costs incurred and the benefits accrued under each mating tactic, to infer how individual males can balance the decision to switch between tactics. To test our hypothesis, we classified reindeer males as harem-holders, sneaking, or mixed tactic males on the basis of their tactic index throughout the rutting season. Then, using direct and indirect measures of mating effort (i.e. body mass loss and activity budgets, respectively; e.g. Mysterud et al., 2004), and measures of mating outcomes (i.e. mating group size and number of offspring sired; e.g. Røed et al., 2002), we assessed the costs and benefits for each mating tactic.

1 Materials and Methods

1.1 Study area and experimental animals

The study was performed at the Kutuharju Field Reindeer Research Station in Kaamanen, Finland (69°N, 27°E). Data were collected daily from 25 September 2012 till 17 October 2012. A semi-domesticated reindeer population, free ranging for most of the year, was located at the Sinioivi fenced enclosure (13.4 km^2; Body et al., 2014). The habitat is characterised by pine *Pinus sylvestris* and birch (*Betula spp.*) forests with several lakes and boggy areas (Mysterud et al., 2003). Reindeer are supplementary fed during winter only (Holand et al., 2003). During the calving season all females were kept within a smaller enclosure (approximately 0.5 km^2) where data on birth date (daily observation) and mother – calf assignments were obtained and the calves were tagged individually (Røed et al., 2002; L'Italien et al., 2012). The reindeer herd was composed of 11 males and 33 females. The male age structure was: 4 adult ($\geq$ 3.5 years old) and 7 young males (< 3.5 years old). The mean female age was 6.39 ± 3.46 years old (mean ± *SD*, *n* = 33). The adult sex ratio (i.e. ASR, the ratio of sexually mature males to sexually mature females; Tennenhouse et al., 2011) was 1:3. All animals were marked with uniquely coded collars. Furthermore, all males and most females were fitted with VHF radio collars.

Similar to previous studies (Holand et al., 2006; Djaković et al., 2012; Tennenhouse et al., 2012) we divided the rutting season, which lasts for approximately three weeks, into three phases: early peak-rut (from 25 September till 29 September), peak-rut (from 30 September till 7 October), and late peak-rut (from 8 October till 15 October). The start of the peak-rut week was established based on the first copulations which were observed, and corresponded to the 30 September 2012.

1.2 Estimation of tactic index

Males were located daily using ground tracking and recorded as harem-holders or sneaking males. A harem-holder was defined as the male within the mating group having control of the harem (Tennenhouse et al., 2011, 2012), whereas a sneaking male usually stood in the proximity and attempted to steal copulation. The tactic

index was calculated using the formula $[HH_i/(HH_i + SN_i)]$, where HH_i is the number of times a male was observed as a harem-holder, whereas SN_i is the number of times a male was observed as a sneaking male. The formula was slightly modified from that described by Willisch et al. (2012), since linearity tests were not performed in our study. We then established two narrow cut-off points defining as harem-holders (HH) individuals whose tactic index was > 0.75, and defining as sneaking males (SN) individuals whose tactic index was < 0.25. As a result, mixed-tactic males (MT) were defined when the tactic index ranged between 0.25 and 0.75. The mean tactic index was also calculated for each mating tactic category, and within each rutting phase, to show mating tactic phenology throughout the rutting season.

1.3 Direct and indirect measures of male mating effort

The males were weighed to the nearest kg both before (first half of September) and after (last half of October) the rutting season. The percentage of body mass lost during the rutting season was assessed as a direct measure of male mating effort (Mysterud et al., 2004). Due to technical problems, the body mass of one male (i.e. R88) could not be assessed after the rutting season. Focal observations were evenly spread during daylight hours (between 10:00 h and 19:00 h) and performed with the aid of binoculars (8 × 40) when the animals were beyond 50 m from the observer (Tennenhouse et al., 2011). In order to assess the activity budgets during the rutting season, focal sampling was conducted during 15 min time periods split into 15 s intervals, at the end of which male behaviour was noted (Tennenhouse et al., 2012). In addition, 1 h focal sampling was conducted on harem-holder males noting all-occurrences behaviour to test relationships between behavioural patterns. For the 15 min and 1 h forms, male activity patterns were categorized as feeding, walking, standing, resting, chasing, herding, displacing, sparring, fighting, courting, attempting to copulate, or copulating (Tennenhouse et al., 2012). Feeding overrides walking if both occur simultaneously (Alados, 1986). Five observers were involved in the present study and they were blind to the aims of the work.

1.4 Outcomes of male mating effort

Mating group size and number of offspring sired were estimated as measures of male mating effort outcomes (e.g. Røed et al., 2002). Mating group size was measured as the number of adult females observed each day with each harem-holder (L'Italien et al., 2012). Blood samples were obtained from all individuals and analyzed for sixteen microsatellite loci as part of an ongoing progeny testing within this experimental herd (Røed et al., 2002). The microsatellites analyzed were NVHRT-01, -03, -16, -31, -48, -66, -73, -76 (Røed and Midthjell, 1998), RT-1, -5, -6, -7, -9, -30 (Wilson et al., 1997), OarFCB193 (Buchanan and Crawford, 1993), and BM4513 (Bishop et al., 1994). Paternity assignment was conducted with the simulation program CERVUS 3.0 (Kalinowski et al., 2007), which is based on likelihood ratios between the candidate sires. We also assessed female body mass before and after the rutting season (86.26 ± 9.40 kg, $n = 31$ and 84.21 ± 8.58 kg, $n = 33$, respectively; mean ± SD), although due to technical problems two females could not be weighed before the rut. Because female body mass before and after the rutting season were highly correlated (Spearman's rank correlation $\rho = 0.892$, $P < 0.001$, $n = 31$), hereinafter we used female body mass after the rut as a proxy measure of female body condition.

1.5 Statistical analysis

Statistical analyses were performed using the SPSS 20.0 statistical software package (SPSS Inc, Chicago, IL, USA). The Shapiro-Wilk test was used to check the normal distribution of the data. The Wilcoxon Signed-Rank test was applied to check for differences between body mass before and after the rutting season. The Mann-Whitney U and Kruskal-Wallis tests were applied to check for differences between two or more independent groups, respectively. The effect of age on the percentage of body mass lost and pre-rut body mass among mating tactics was assessed by including it as a covariate. Generalized linear mixed models (GLMMs), fitted with Poisson distribution with a logarithmic link, were applied on activity budgets (15 min forms) to assess the effect of rutting phases (factor with three levels), male mating tactics (factor with three levels), and interactions between fixed factors on male behaviour. The identity of males was used as a random factor to avoid pseudoreplication, because several males were observed more than once. The covariance structure of random factor was estimated in several ways (e.g. first-order autoregressive, autoregressive moving average, compound symmetry, diagonal, Toeplitz, and unstructured), and based on information criteria (AIC_c, BIC) we selected the best fit for the final models (i.e. scaled identity). The degrees of freedom were calculated according to the Satterthwaite approximation (Bolker et al., 2008). The two-tailed Spearman's rank correlation test was applied to determine the relationships between variables (i.e. individual traits and activity patterns from 1 h forms)

averaging the frequency of behaviours for each male to avoid pseudoreplication. Since feeding, standing, and walking frequencies occurred considerably more than the other activities, only these variables were used for the analyses.

2 Results

2.1 Estimation of tactic index

Descriptive statistics of the individual traits of reindeer males are shown in Table 1. On the basis of the tactic index, we classified four males as harem-holders, four as sneaking males, and three as mixed-tactic males (Table 1). Overall, the mixed-tactic males showed their highest tactic index during the peak-rut, while harem-holders showed their highest tactic index during the early peak-rut and peak-rut (Fig. 1). On the other hand, sneaking males showed a constant zero value for their tactic index through the rutting season (Fig. 1).

2.2 Direct measures of male mating effort

Reindeer males significantly reduced their body mass during the rutting season (105.40 ± 36.23 kg and 97.00 ± 27.27 kg before and after the rutting season, respectively; mean ± SD, $n = 10$, $Z = -2.405$, $P = 0.016$). Harem-holders lost significantly more body mass than sneaking males ($P = 0.015$; Table 2), although the differences were not significant after controlling for age ($P = 0.078$; Table 2). Sneaking males lost minimal to no body mass, and two sneaking males (both 1.5 year old) even increased their body mass by 2% during the mating season. The percentage of body mass lost by mixed-tactic males was intermediate between the highest values of harem-holder males and the lowest values of sneaking males, although the differences were not statistically significant ($P = 0.675$ and $P = 0.390$, respec-

tively; Table 2).

The percentage of body mass lost was significantly lower for young than adult males, ranging from 2.67% in a 1.5 year old young male to 17.61% in a 4.5 years old adult male ($W = 28.00$, $P = 0.017$; Table 2). As shown in Table 2, pre-rut body mass was significantly higher in harem-holders than in sneaking males ($P = 0.023$), whereas no significant difference was found with respect to mixed-tactic males ($P = 0.227$). The effect of mating tactic was nevertheless not significant after controlling for age ($P = 0.111$; Table 2).

Age was positively associated with the harem-defense tactic, since the harem-holders were significantly older than the sneaking males ($P = 0.015$; Table 2). Age was also positively related to pre-rut body mass and to the percentage of body mass lost during the rutting season ($\rho = 0.885$, $P < 0.001$, $n = 11$ and $\rho = 0.847$, $P = 0.002$, $n = 10$, respectively). Moreover, the percentage of body mass lost was positively related to the pre-rut body mass ($\rho = 0.842$, $P = 0.002$, $n = 10$).

2.3 Indirect measures of male mating effort

Overall eighty-two 15 min and fifty-one 1 h forms were collected during this study. The effects of the rutting phases, mating tactics, and the interactions between the fixed factors are shown in Table 3. Harem-holders and mixed-tactic males fed significantly less during the peak-rut ($P = 0.003$ and $P < 0.001$ for harem-holders; $P = 0.002$ and $P = 0.001$ for mixed tactic males) compared to both the early peak-rut and late peak-rut, respectively (Fig. 2A), whereas sneaking males fed less during the late peak-rut ($P = 0.039$ and $P = 0.002$) compared to the early peak-rut and peak-rut, respectively (Fig. 2A). Moreover, the frequency of standing tended to be constant in mixed-tactic males, without any significant dif-

Table 1 Descriptive statistics of reindeer males used in the present study

ID	Age (yr)	Pre-rut BM (kg)	Post-rut BM (kg)	BM variation (%)	Tactic index (0–1)	Mating tactic
R02	1.5	83	79	-4.82	0.63	MT
R78	1.5	75	73	-2.67	0.00	SN
R80	4.5	140	117	-17.61.	0.92	HH
R82	6.5	173	153	-11.56	1.00	HH
R84	3.5	150	130	-13.33	1.00	HH
R88	4.5	140	n.a.	n.a.	1.00	HH
R90	2.5	108	97	-10.19	0.25	MT
R92	1.5	79	76	-3.80	0.25	MT
R94	1.5	82	84	+2.44	0.00	SN
R96	1.5	86	83	-3.49	0.00	SN
R98	1.5	76	78	+2.63	0.00	SN

BM: Body mass. HH: harem-holders; MT: mixed-tactic males; SN: sneaking males. n.a.: not available.
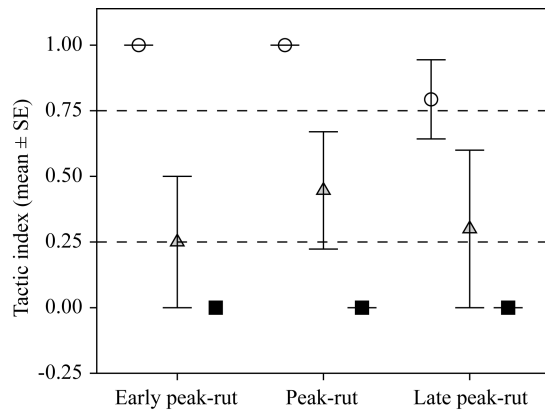
Fig. 1   Mating tactic phenology during the rutting season in reindeer males
Bars show mean ± *SE* of the tactic index in harem-holders (white circles; *n* = 4), mixed-tactic males (grey triangles; *n* = 3), and sneaking males (black squares; *n* = 4). Only one sneaking male was observed in the early peak-rut. Dotted lines show the cut-off between the mating tactic categories.

Table 2   Descriptive statistics of age and direct measures of mating effort in reindeer during the rutting season according to the mating tactic

Mating tactic	Pre-rut BM (kg)	BM variation (%)	Age (yr)	*n*
HH	155.00 ± 16.10*	-14.17 ± 3.11*[1]	4.8 ± 1.5*	4
MT	90.00 ± 15.72	-6.27 ± 3.43	1.8 ± 0.6	3
SN	79.75 ± 5.19*	-0.27 ± 3.26*	1.5 ± 0.0*	4

Data are shown as the mean ± *SD*. Symbols within the same column are statistically different (*P <0.05). Pre-rut BM and BM variation were not statistically different among the mating tactics after controlling for age (*P* >0.05).[1]Data from three males. BM: Body mass. HH: harem-holders; MT: mixed-tactic males; SN: sneaking males.

ferences among the rutting phases (all *P* > 0.05; Fig. 2B). By contrast, harem-holders stood significantly more during the early peak-rut and peak-rut (*P* = 0.017 and *P* = 0.011) compared to the late peak-rut, respectively (Fig. 2B), whereas sneaking males increased their standing frequency during the late peak-rut (*P* = 0.013) compared to both the early peak-rut and peak-rut (Fig. 2B). The mixed-tactic males and harem-holders walked significantly more in the early peak-rut and peak-rut, respectively (*P* = 0.043 and *P* = 0.023), compared to the late peak-rut (Fig. 2C), while sneaking males showed constant walking frequency values across the rutting phases (all *P* > 0.05; Fig. 2C). Correlation analysis showed that the proportion of time spent walking was positively correlated to standing activity (*ρ* = 0.821, *P* = 0.023, *n* = 7), whereas no significant correlation was found among the other activity patterns (all *P* > 0.05).

Table 3   Effect of rutting phase, mating tactic, and the interaction between them on the behaviour of reindeer males (*n* = 82 observations)

	F	*df1*	*df2*	*P*
Feeding				
Corrected model	14.521	8	55	**<0.001**
Rutting phase	15.125	2	73	**<0.001**
Mating tactic	4.830	2	9	**0.039**
Mating tactic*Rutting phase	18.068	4	73	**<0.001**
AIC$_c$ (587.337), BIC (589.571)				
Standing				
Corrected model	10.902	8	32	**<0.001**
Rutting phase	3.311	2	73	**0.042**
Mating tactic	2.072	2	8	0.186
Mating tactic*Rutting phase	17.797	4	73	**<0.001**
AIC$_c$ (657.646), BIC (659.880)				
Walking				
Corrected model	5.831	8	26	**<0.001**
Rutting phase	2.183	2	73	0.120
Mating tactic	11.713	2	6	**0.007**
Mating tactic*Rutting phase	0.638	4	73	0.637
AIC$_c$ (268.175), BIC (270.409)				

AIC$_c$: Corrected Akaike Information Criterion. BIC: Bayesian Information Criterion.

2.4   Outcomes of male mating effort

Twenty-nine calves were born from 4 May 2013 to 21 May 2013 (calving rate: 87.88%) and were assigned a sire with high statistical confidence (> 95%). As shown in Fig. 3, reproductive success varied greatly between individuals, and offspring number generally corresponded to the mating group size (*ρ* = 0.741, *P* = 0.057, *n* = 7). Overall, the mating group size and number of calves sired were higher in harem-holders than in mixed-tactic males (mating group size: 8.30 ± 4.69 vs. 3.61 ± 0.35; offspring number: 6.75 ± 5.32 vs. 0.67 ± 0.58; mean ± *SD*, *n* = 4 and *n* = 3, respectively), although the differences were not statistically significant (*P* = 0.400 and *P* = 0.114, respectively). Paternity analyses showed that all harem-holders successfully sired at least one calf. Reproductive success varied greatly between harem-holders, ranging from 1 calf sired by R88 to 13 calves sired by R80, despite the fact that they were both 4.5 years old. On the other hand, two out of three mixed-tactic males sired one calf, whereas sneaking males did not sire any calves. Both calves sired by mixed-tactic males were born late in the calving season (i.e. 18 May 2013). Additionally, females fecundated by mixed-tactic males tended to be older and in poorer

condition than those fecundated by harem-holders (female age: 8.50 ± 3.54 years old vs. 6.22 ± 3.26 years old, female body mass: 77.50 ± 6.36 kg vs. 85.37 ± 8.40 kg; mean $\pm$ SD, $n = 2$ and $n = 27$, respectively).

3 Discussion

Our results show that reindeer males may switch between the harem-defense and the sneaking tactics throughout the same breeding season. This provides further support to the notion that, across ungulates, males rarely show irreversible patterns, but often switch between two or more mating tactics (Isvaran, 2005). The costs and benefits of male mating effort vary according to the mating tactic, reaching the highest values in harem-holders and the lowest values in sneaking males. Our results support that males who switch between reproductive tactics can achieve higher mating payoffs than males who consistently use the least demanding tactic (Bro-Jørgensen, 2011a).

Mating tactics in polygynous ungulates are usually size- or weight-dependent, or both, and therefore also age-dependent (Mysterud et al., 2001; Mainguy et al., 2008; Willisch and Neuhaus, 2009, L'Italien et al., 2012), making the effect of each factor difficult to separate (Mysterud et al., 2004). Mixed-tactic males showed intermediate values for age and body mass, between the oldest and largest harem-holders and the youngest and smallest sneaking males. Our results are nevertheless not decisive in this respect because of the small sample size and the uneven distribution of males of various ages. Overall activity budgets indicate that harem-holders and mixed-tactic males invest most of their effort during the early- and peak-rut, whereas sneaking males invest most of their effort during the late peak-rut. The investment from most competitive males during the early-rut might be explained by their effort to herd females and increase their harem size before the peak-rut (Body et al., 2014), when most females are
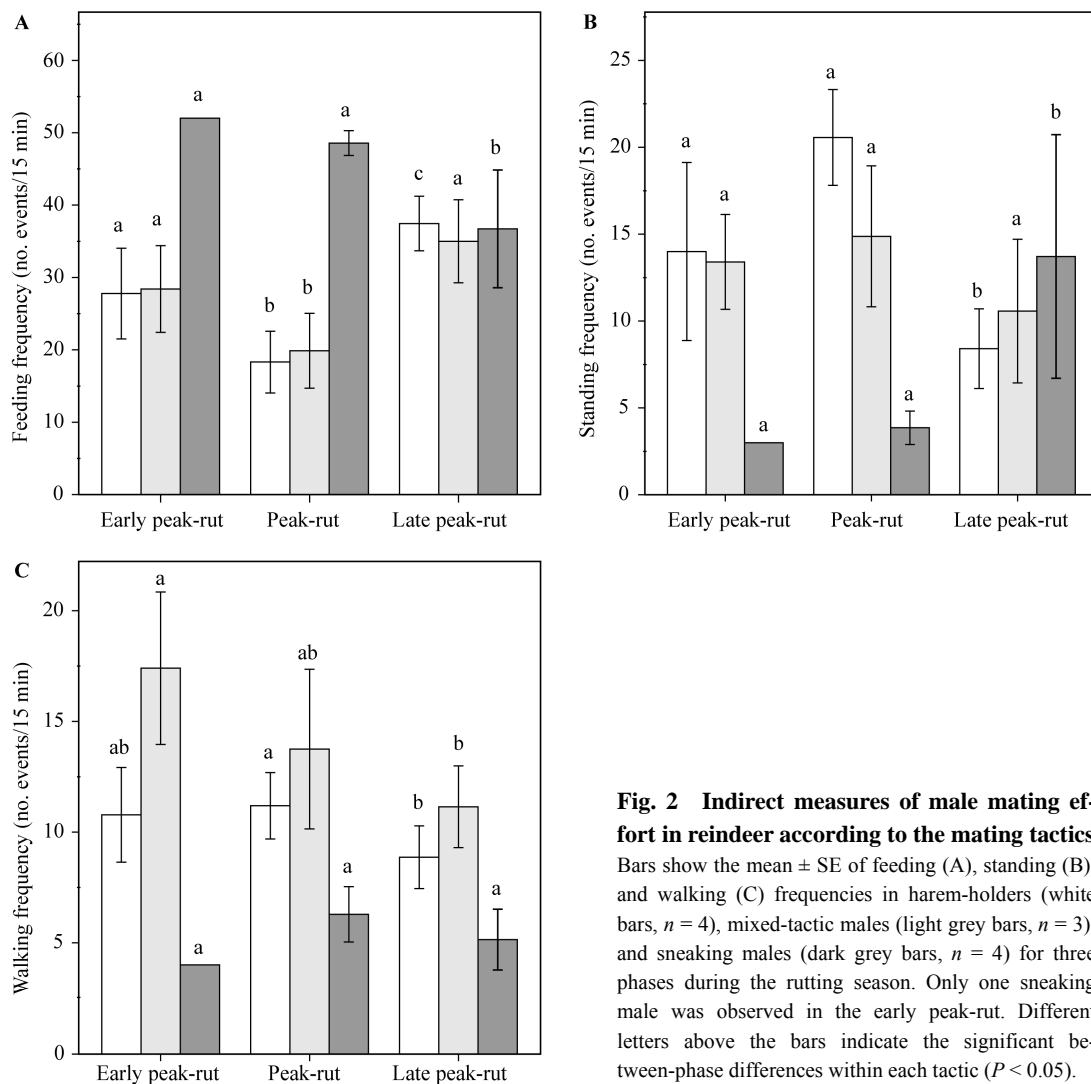

Fig. 2   Indirect measures of male mating effort in reindeer according to the mating tactics Bars show the mean $\pm$ SE of feeding (A), standing (B), and walking (C) frequencies in harem-holders (white bars, $n = 4$), mixed-tactic males (light grey bars, $n = 3$), and sneaking males (dark grey bars, $n = 4$) for three phases during the rutting season. Only one sneaking male was observed in the early peak-rut. Different letters above the bars indicate the significant between-phase differences within each tactic ($P < 0.05$).
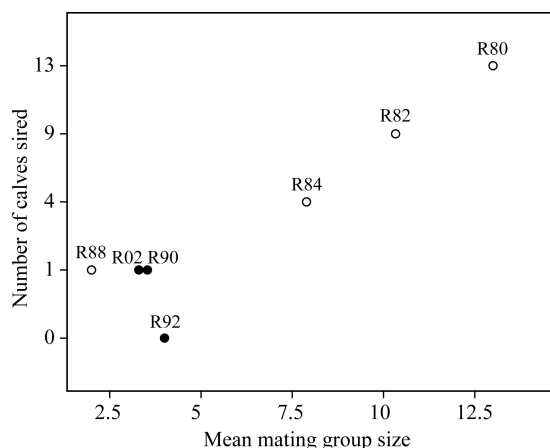
Fig. 3 Reproductive success in reindeer males using different mating tactics

The relation between the number of calves sired and the mean mating group size in harem-holders (open circles) and mixed-tactic males (filled circles).

likely to be in oestrus and, as a consequence, the chances of fertilization success are higher (Preston et al., 2003; Tennenhouse et al., 2012). Conversely, sneaking males invest most of their energy during the late phase of rutting when harem-holder males are likely to be exhausted because of the high reproductive effort spent; as a result, sneaking copulations might be more successful (Clutton-Brock et al., 1982; Mysterud et al., 2008). Our findings also support that alternative mating tactics are associated with different patterns in foraging behaviour as recently proposed by Corlatti and Bassano (2014). By contrast, in bighorn rams, Pelletier (2005) found that foraging behaviour was independent of mating tactic, although in the same study, the proportion of time spent foraging by males who switched between tending and coursing varied according to the tactic adopted. We found that, although sneaking males significantly reduced their feeding frequency in the late peak-rut, this was of inconsequential as they lost little to no body mass. Perhaps the decreased feeding time is due to the concurrent increase in standing behaviour. Standing is regarded as a part of active behaviour (Maher and Byers, 1987), and often associated with female defense because it allows a harem-holder male to watch members of the group and stay alert to herd females or to chase away intruding males (Tennenhouse et al., 2012 and references therein). Conversely, the standing frequency in sneaking males might be associated with the increased effort to sneak copulations. Accordingly, our results show that standing frequency was higher during the early peak-rut and peak-rut in harem-holders, whereas sneaking males stood significantly more during

the late peak-rut. Males with mixed reproductive tactics show constant values for standing frequency during the entire rutting season, because standing implies for them defending the harem or sneaking copulations, according to the circumstances.

Mating success showed the same trend as mating effort. Thus, mixed-tactic males showed intermediate values of mating outcomes between the highest mating group size and number of calves sired by harem-holders and the failure of sneaking males. Mating group size and reproductive success tended to be higher in harem-holders than in mixed tactic males, although the differences were not significant as a likely consequence of the small sample size. Our results are consistent with previous studies indicating that variance in male reproductive success is remarkable (Clutton-Brock et al., 1988), and generally corresponds to high mating group size (Coltman et al., 1999). Our results also show that offspring of harem-holders were born throughout the whole calving season, while the two calves sired by mixed-tactic males were born late in the season, suggesting that copulation attempts by mixed tactic males were more successful in the late rutting season. We have to take into account, nevertheless, that gestation length may vary considerably in reindeer as a function of maternal, foetal, and environmental factors (Mysterud et al., 2009; Shipka and Rowell, 2010), which may weaken the link between the dates of conception and calving. Among the maternal factors, the timing of ovulation is strongly affected by maternal age and body mass (in reindeer: Ropstad, 2000; in red deer: Langvatn et al., 2004). We found that females fecundated by mixed tactic males tended to be older and in poorer condition than those fecundated by harem-holders, though the uneven distribution of cases between the groups did not allow for any powerful statistical analysis to be conducted. Therefore, it is likely that copulation attempts by mixed-tactic males were more successful in the late rutting season when most competitive males might be exhausted or sperm depleted (Preston et al., 2001). Under such a scenario, nevertheless mate sampling and choice may also play a role: females may increase their sampling of mates to ensure fertilization success (Briefer et al., 2013), or they may look for preferred males for direct and indirect benefits (Bro-Jørgensen, 2011b).

Our analysis has focused on the influence of individual traits, but the effects of social environment may also affect mating tactic election (Isvaran, 2005). For instance, the mating success of young males may increase when the adult sex ratio (ASR) is strongly female

biased (Mysterud et al., 2003, 2004), or when strong competition between males does not allow them to maintain effective control over their harems, increasing the opportunities for sneaking males (Røed et al., 2002). Our results suggest that reindeer males may switch between the harem-defense and sneaking tactics to take the advantage of the social environment, however our study is limited to only one rutting season when social conditions such as ASR are constant. Further research on a long-term basis will help to confirm our findings and show how inter-annual variations in conditions may affect mating tactics, and also show how flexible tactics may contribute to the lifetime reproductive success of individual males.

In conclusion, our study shows that reindeer males may switch between the harem-defense and sneaking tactics across the same breeding season, as a function of their condition and probably of their relative chances with respect to rivals throughout the rutting season, and represents a first attempt to estimate mating effort and benefits associated with mating tactics in reindeer.

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